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The foraging behavior, habitat use, and diet of arctic foxes (*Alopex lagopus*) in a goose nesting area near Kokechik Bay, Alaska

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THE FORAGING BEHAVIOR, HABITAT USE, AND DIET OF ARCTIC FOXES (ALOPEX LAGOPUS) IN A GOOSE NESTING AREA NEAR KOKECHIK BAY, ALASKA

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A
THESIS

MASTER OF SCIENCE

By
Alice A. Stickney, B.A.
Fairbanks, Alaska
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ABSTRACT

The foraging behavior, habitat use, and diet of arctic foxes were observed in a goose nesting area near Kokechik Bay, Alaska during the summers of 1985 and 1986. The foraging patterns of arctic foxes changed after birds started nesting in the study area, adding an abundant egg resource to a previously limited prey base. The duration of search bouts decreased and success rate increased, yielding an increased prey capture rate. Over 80% of the eggs taken by foxes during the nesting stage were cached, rather than eaten immediately. Differences in search patterns among foxes were probably related to the different prey available within the range of each fox. Egg caches extended fox access to a temporally clumped resource, and increased the impact of foxes on the nesting success of geese. Eggs were the primary prey of foxes during the nesting stage in both years, regardless of variations in microtine abundance.

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INTRODUCTION

Arctic foxes (Alopex lagopus) are small canids with a circumpolar distribution and a diet that is strongly influenced by seasonality in prey availability (Chesemore 1967, Stephenson 1970, Eberhardt 1977). Although effective generalist predators, their influence on their prey varies. In the tundra regions of their range, fox numbers seem to be regulated by the population levels of their small mammal prey, particularly lemmings (Lemmus spp. and Dicrostonyx torquatus) (Braestrup 1941, Elton 1942, Shibanoff 1958, Macpherson 1969), rather than the converse. However, some researchers have suggested that predation by arctic foxes on birds is so important that it may influence the location of seabird colonies (Turner 1886, Fay and Cade 1959), and the distribution and habitat selection of other birds which nest in the Arctic (Larson 1960).

Early research on the arctic fox suggested that small mammals were the primary prey of these canids and a dietary divergence toward a dependence on seabirds and other marine-related prey was a function of color phase differences; blue-phase "coastal" or island foxes seem to depend on birds more than do mainland white-phase foxes (Braestrup 1941). The diets of white-phase foxes on St. Lawrence Island are variable and are related to habitat and prey availability, rather than color phase (Stephenson 1970). Elsewhere in arctic Alaska and Canada, small mammals are important in the summer diet of arctic foxes (Chesemore 1968, Macpherson 1969, Stephenson 1970, Speller 1972, Garrott 1980, Garrott et al.

1983), with indications that birds become a large component of the diet in years when lemming numbers are low (Eberhardt 1977, Garrott 1980, Burgess 1984).

The effect of arctic foxes and other generalist predators on the success of arctic nesting waterfowl can be especially severe (Barry 1967, Ryder 1969, MacInnes and Misra 1972, Quinlan and Lehnhausen 1982, Sedinger 1984). In certain years, many or all of the eggs produced in some local colonies have been destroyed; migrating foxes are apparently responsible for any large-scale destruction of eggs in the Arctic (MacInnes and Misra 1972, Quinlan and Lehnhausen 1982). The caching of eggs is the principal reason foxes are capable of such major reductions in the nesting success of waterfowl (Barry 1967).

Arctic fox predation may also be influential in limiting the expansion of colonies of birds such as snow geese (Chen caerulescens; Syroechkovskii 1972). The impact on individual nests is generally sporadic, except in years of low lemming populations (Barry 1967), and is focused primarily on peripheral nests (Syroechkovskii 1972).

While there have been several studies on the food habits of arctic foxes, only a few studies have focussed on their foraging behavior and these have been conducted in areas of arctic Alaska and Canada where waterfowl nested in low densities (Speller 1972, Burgess 1984). In contrast, the Yukon-Kuskokwim (Y-K) Delta in subarctic, southwest Alaska is an area where the range of the arctic fox coincides with a major breeding area for many species of migratory birds, especially waterfowl (Spencer et al. 1951). It is the primary nesting area for emperor geese (Anser canigicus) (Eisenhauer and Kirkpatrick 1977), black brant (Branta bernicla nigricans) (Spencer et al. 1951, Byrd et al. 1982), and greater white-fronted geese (Anser albifrons frontalis) (Spencer et al. 1951, Mickelson 1975, Bellrose 1976), and is the only breeding area for cackling Canada geese (Branta canadensis minima)

(Bellrose 1976). Since the late 1960's, the populations of all four of these geese have declined (O'Neill 1979). Overharvest by humans is the principal cause of the decline (Raveling 1984, King and Derksen 1986, Pamplin 1986), but predation by both mammals [arctic fox, red fox (Vulpes vulpes), mink (Mustela vison), etc.] and birds [glaucous gull (Larus hyperboreus) and parasitic jaeger (Stercorarius parasiticus)] has limited the recovery of the goose populations (Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Petersen 1982, Sedinger 1984, Pamplin 1986). Arctic foxes were the most serious non-human predator on nesting geese in Mickelson's study area on the Y-K Delta in 1975. By 1984, it was evident that arctic fox predation was significantly reducing goose nesting success in several areas of the Y-K Delta (Petersen 1984, Sedinger 1984, Stehn 1986).

In view of the low populations of geese in the Y-K Delta and the reported contribution of arctic foxes to the decline, I sought to collect specific information on their foraging behavior, selection of foraging habitat, and summer diet. Despite the extensive research that has been done on arctic foxes in other areas of their range, little is known about their ecology on the Y- K Delta. The studies by Speller (1972) and Burgess (1984) on arctic foxes in northern Alaska and Canada demonstrated that resource availability varied among habitat types and that foxes allocated time and hunting intensity differently among the different habitats. In the Y-K Delta, the four species of geese have distinct patterns in density and habitat use during nesting (Bellrose 1976, Mickelson 1975, Eisenhauer and Kirkpatrick 1977), and small mammals also show habitat preferences (Tast 1966, Kostlan 1970, Anthony et al. 1985, 1987). I collected information on the interaction between the foraging behavior of foxes and their use of habitats to determine whether changes in the available prey base altered either of the two. This study was part of a larger research

effort by the U.S. Fish and Wildlife Service on arctic foxes in the Y-K Delta (Anthony et al. 1985, 1987).

The objectives of my research were to:

1) Observe the foraging behavior of arctic foxes near Kokechik Bay, Alaska, and determine the relationship of any changes in that behavior to seasonal and annual changes in the available prey base;

2) Determine the proportion of foraging time foxes allocated to various habitats in the study area and their behavior in those habitats;

3) Assess the summer food habits of arctic foxes in the study area.

Between 12 May-12 August 1985, and 4 May-22 July 1986, I made behavioral observations of arctic foxes, collected fox scats and prey remains, and sampled microtine abundance in different habitats. I subsequently worked for the U.S. Fish and Wildlife Service during the summer of 1987, which provided additional perspective on the data gathered during the previous two years.

STUDY AREA

This study was conducted near Kokechik Bay on the Y-K Delta (Fig. 1). Kokechik Bay (210 km WNW of Bethel) was the northern boundary of the study area; east-west oriented bluffs 4.5 km south of the bay were the southern boundary. A large lake which was the site of another research camp was the eastern limit; the western limit of the area was approximately 3 km west of the camp site. The study area was approximately 36 km^2 in 1985, but was reduced to 13.5 km^2 in 1986, centered around two observation towers located on a north flowing slough (Tower 1 and 2b; Fig. 2).

The average annual temperature for the Y-K Delta is -1°C; the annual precipitation is 95 cm, 41 cm in rain and 54 cm in snow [NOAA (National Oceanographic and Atmospheric Administration) 1984]. The average summer temperatures for the study area range from -1 in May to 8° C in July (NOAA 1984). In 1985 the average temperature was cooler than normal in April (by 9°C) and May (by 3°C), prolonging break-up and delaying nest initiation for geese (NOAA 1985). In 1986, temperatures were about average for the late spring and summer months (NOAA 1986).

The habitat of the study area is tundra, characterized by poorly drained soils covered by peat mats [Arctic Environmental Information and Data Center (AEIDC) 1977]. The area is underlain by discontinuous permafrost 25-50 cm below the surface (Jackson 1981). Ice mounds and peat deposits in depressions are common

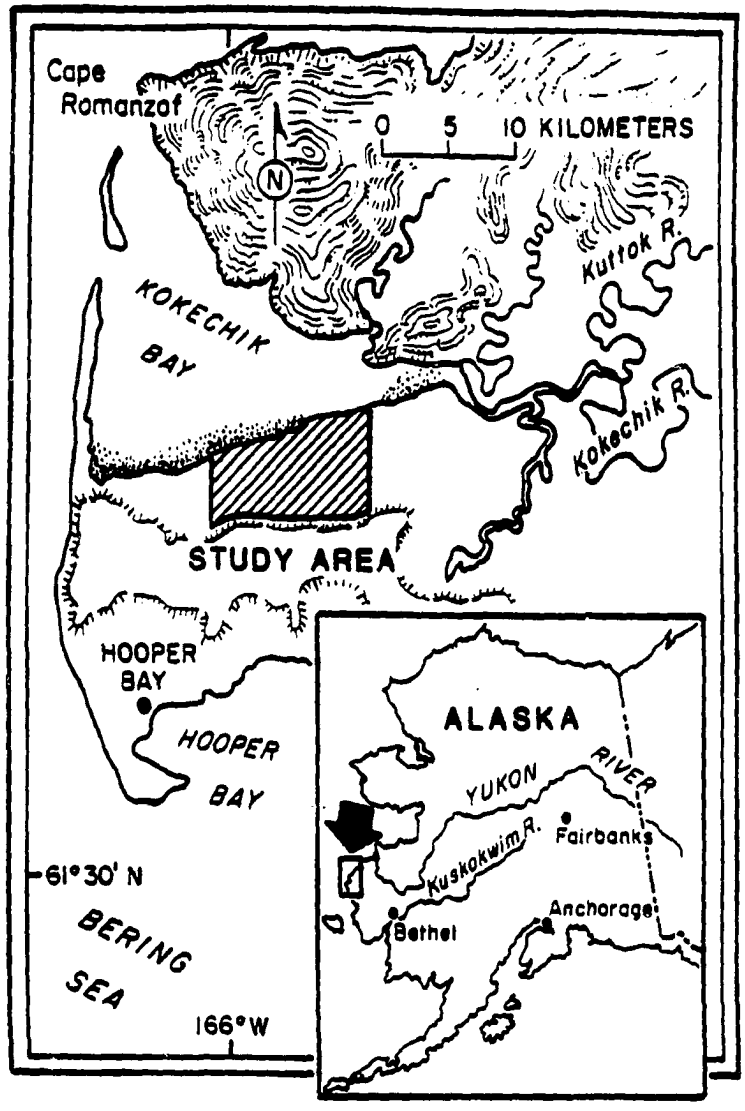

Fig. 1. Map of Alaska showing the location of the Kokechik Bay study area (hatched).

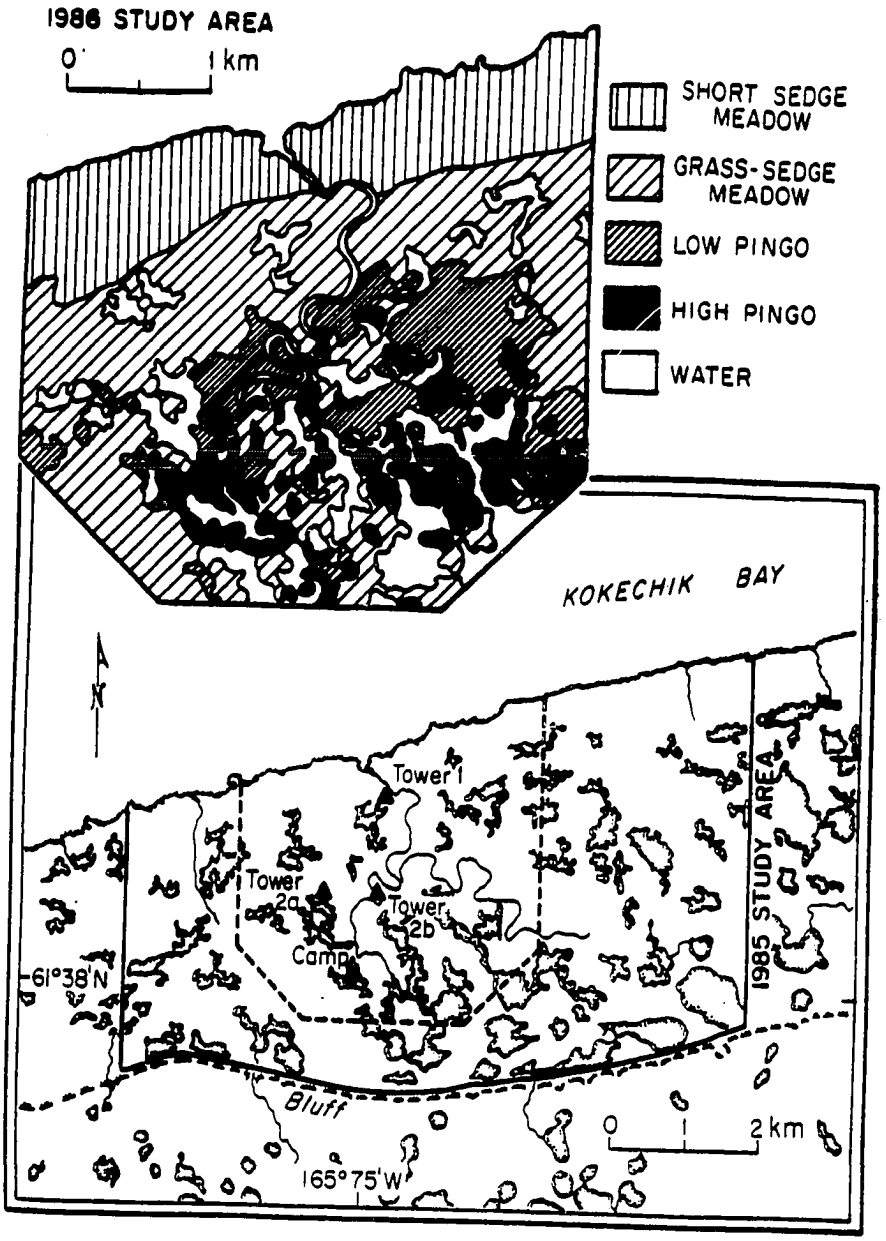

Fig. 2. Map of the 1985 (below) and 1986 (above) study areas near Kokechik Bay, Alaska. The locations of the towers used to make behavioral observations are shown in the lower map and the vegetation zones in the 1986 study area are indicated in the upper map.

(AEIDC 1977). Thirty to 50% of the area is covered by thaw lakes; drainage is provided by low gradient, meandering streams (Wahrhaftig 1965).

The Kokechik Bay area has 10 different vegetation zones which roughly form a continuum along a north-south gradient (Jackson 1981); the 1986 study area included four of these zones (Fig. 2). Bordering Kokechik Bay is the short sedge meadow (SSM) zone which is relatively flat (less than 1 m above high tide), punctuated by numerous shallow ponds, and drained by small tidal sloughs. This zone (24% of the 1986 study area) contains areas of bare mud which are maintained by tides. The plant community (7 spp.) is dominated by small-statured Carex rariflora (Jackson 1981) and C. ramenskii (Anthony et al. 1987). Inland, the elevation increases slightly, resulting in development of grass-sedge meadows (GSM zone; Fig. 2). Here the land is relatively flat, but there is a scattering of low mounds less than 0.5 m in height and better drainage than the short sedge meadow. Grasses (5 spp.) and sedges (5 spp.) dominate the plant community (Jackson 1981). This zone represented 41% of the 1986 study area.

Along the southern edge of the grass-sedge meadow, low pingos less than 3 m high occur, resulting from ice lens expansion (Wahrhaftig 1965) and forming the low pingo (LP) zone (Jackson 1981; Fig. 2). This zone composed 16% of the 1986 study area. The ponds in this zone are deep (>0.5 m) and drain into large tidal sloughs. Lichens, mosses, and ericaceous species are dominant plants. Grasses and sedges are generally restricted to the bases of pingos and disturbed sites (Jackson 1981). Inland of the low pingos is the high pingo (HP) zone (13% of the 1986 study area; Fig. 2). The pingos in this zone are up to 6 m high and a few hundred meters in length. In addition to ericaceous plants, lichens, and mosses, the high pingos also support shrub willow (Salix) species and dwarf birch (Betula nana). The

diversity of the plant communities is greatest in the pingo zones (40 spp. in the high pingos and 33 spp. in the low pingos) (Jackson 1981).

These vegetation zones are mosaics of different habitat features (defined here as microhabitats) including slough and pond shores, grass meadows, islands, pingo sides, and pingo tops. The heterogeneity of the habitat in the Kokechik Bay region is paralleled by the high diversity of wildlife species which use the area, including year-round residents (Stickney 1986) as well as a large number of summer migrants, mostly birds (Holmes and Black 1973). The largest colony of black brant in the Y-K Delta is in this area (Byrd et al. 1982) with an estimated average density of 3.5 nests/ha for all vegetation zones examined in 1986 (D. Ward, unpublished data) and 15 nests/ha in areas of high density (Thompson and Raveling 1987). In addition, the Kokechik Bay region supports nesting by large numbers of other geese, shorebirds, other waterfowl, gulls, and passerines (Holmes and Black 1973, Eisenhauer and Kirkpatrick 1977). Estimated densities for other birds include 0.02 nests/ha for cackling Canada and emperor geese, 0.004 nests/ha for greater white-fronted geese (Stehn 1987), 0.75 pairs/ha for dunlin (Calidris alpina), and 5.0-7.5 pairs/ha for western sandpipers (Calidris mauri) (Holmes and Black 1973).

The use of the various vegetation zones and even microhabitats within the zones for nest sites or burrows differs among species. Brant and cackling Canada geese reach their highest nesting densities in the short sedge meadow zone (15 nests/ha for brant) (Thompson and Raveling 1987). Within this zone we observed them to preferentially nest along shores and islands with low vegetation, although brant also used grass meadow sites. Emperor geese, ducks, shorebirds, glaucous gulls and parasitic jaegers were also observed to nest in this zone.

Brant and cackling Canada geese also nest in the grass-sedge meadow along with emperor geese, but brant are generally found in lower densities in this habitat

than in the short sedge meadow (Kertell 1985). Within the grass-sedge meadow zone emperor geese select slightly elevated sites such as hummocks and scour biocks (Eisenhauer and Kirkpatrick 1977). Neither of the meadow zones provide suitable habitat for microtine rodents (Anthony et al. 1987) and fox dens were uncommon due to the limited number of available mounds (Anthony et al 1985).

Low densities of greater white-fronted and emperor geese nest in the pingo zones. A few cackling Canada geese and brant nested in the low pingo zone, but they were not observed in the high pingo zone. Within the pingo zones, we observed the nests of white-fronted geese in high grass cover along the sides of pingos and in decumbent vegetation on the tops of pingos. In contrast to Ely and Raveling's study (1984), these geese were not observed in "lowland" habitat in the study area. Other nesting species in the pingo zones included willow ptarmigan (Lagopus lagopus), Sabine's gulls (Xema sabini), long-tailed jaegers (Stercorarius longicaudus), passerines, and shorebirds.

The pingo zones provide suitable habitat for tundra voles (Microtus oeconomus) (Tast 1966) and are the principal denning habitat for arctic foxes. The low pingos support low numbers of microtines and contain some den sites for arctic foxes (Anthony et al. 1985, 1987). Microtines reach their highest densities in the high pingo zone (Anthony et al. 1985). Tundra voles prefer tall grass areas that border ponds (Tast 1966, Kostian 1970), with burrows and runway systems along the sides of pingos. All fox dens which were used for whelping in 1985 were in the high pingo zone, but rearing dens were found in both pingo zones (Anthony et al. 1985).

METHODS

Tower Observations

I made observations in both years from two 3 m high portable metal towers equipped with canvas blinds and zippered windows on all sides. One tower was located on a 0.5 m high mound at the interface of the short sedge and grass-sedge meadow zones along the west bank of a major slough and within 400 m of Kokechik Bay (Tower 1; Fig. 2). In 1985 the second tower was on a 0.5 m high mound on the north bank of a pond (Tower 2a; Fig. 2). In 1986 it was moved 900 m east to a 1.5 m high pingo on the west bank of the slough to provide better visibility of nearby denning habitat (Tower 2b; Fig. 2). In both years this tower was in the low pingo habitat near the edge of the high pingo habitat.

I made observations using 22x spotting scopes and 7x35 binoculars. Observation time totalled 73 and 300 person hours in 1985 and 1986, respectively. In 1985 I made observations primarily during 2-4 h late evening shifts [between 2000-0100 h Alaska Daylight Time (ADT)] from 17 May to 8 July. In 1986, I and an assistant made simultaneous observations from the two towers during 36 late evening periods (4 h each) and 17 early morning periods (3 h each between 0500-0900 h ADT) between 6 May and 8 July. These periods corresponded with the daily

periods of maximum arctic fox activity on the study area (Anthony et al. 1987) and elsewhere (Speller 1972, Burgess 1984)

During each observation period, we scanned the area within a 1.6 km radius of each tower continuously until a fox was sighted. We used VHF radios to communicate between our towers and the U.S. Fish and Wildlife Service radio-tracking stations to facilitate location of animals. In 1985, I qualitatively described the fox activity I observed and sampled fox behavior instantaneously at 30 s intervals. The former method did not lend itself to quantitative analysis of behavior, and the 30 s sampling intervals chosen were too long to collect meaningful information on foraging events and were subject to the sampling errors noted by Jacobsen and Wiggins (1982) and Tacha et al. (1985). Accordingly, in 1986 we sampled behavior continuously, recording the time of change (to nearest 1 s) in the fox behavior, and in the microhabitats and vegetation zones in which they occurred. We also recorded all prey caught by foxes and how they were handled. If 2 foxes were within view, the closer one was chosen for observation.

All categories were coded for quick data transcription and were logged onto paper by hand; time was recorded using a digital watch. Whenever possible, foxes were individually identified at the time they were first observed. The U.S. Fish and Wildlife Service researchers in the study area captured foxes, fitted them with radio-collars, and put colored polyvinyl earflags in their ears to aid in identification (Anthony et al. 1985, 1987). In 1985, 2 out of 4 known foxes in the observation areas had radio-collars and earflags. In 1986, 3 foxes in the study area were radio-collared by May, with all 7 known individuals marked by June. In both years, we identified animals during observations by a combination of ear flags, collar markings, radio frequencies, molt patterns (short-term), range locations, and distinctive physical traits.

We terminated data collection if (1) the fox was greater than 1.6 km away or out of view for more than 5 min, (2) the fox's behavior was disrupted by human activity (usually within 800 m), or (3) environmental conditions, such as winds greater than 30 km/h or insufficient light, precluded accurate data collection.

Fox Behavior

I collected data on the frequency, duration, and success of foraging events by arctic foxes during the summer, in order to examine the relationship between foraging behavior and the available prey base. During data collection, I classified behaviors into the following categories, modified from Burgess (1984):

Travel: General long-distance movement by a fox at a loping trot or faster. This category also included swimming, and corresponded to the "search" behavior defined by Burgess (1984).

Search (Forage): Movement by a fox at a walk or slower, often with head lowered and intensive investigation of an area smaller than a few meters in diameter. This category corresponded to Burgess' (1984) "slow search" and included prey capture behaviors such as digging, pouncing and chasing. A search was classified as successful if the fox captured prey. Unsuccessful searches were those in which a fox left the area of investigation or otherwise changed its behavior without capturing prey, in effect "giving up" (Krebs et al. 1974).

Eat: The chewing, swallowing and/or licking of a prey item.

Cache: The burial or retrieval of a prey item in a cache.

Maintenance: This category included grooming, scratching, resting, rolling, urinating, and defecating.

Interspecific interactions: Aggressive behavior by a fox toward, and its response to, aggressive or defensive behaviors by another animal. This category included lunges made by foxes attempting to drive large birds (some geese, cranes, etc.) from their nests.

Intraspecific interactions: Behaviors such as barking, rolling, running away, greeting, and playing, in response to the presence of another fox.

I used the data collected during 1986 to calculate the duration of each behavior and the number and types of prey captured by foxes. I observed that prey availability to foxes could be separated into at least two stages (Table 1). The first stage, "pre-nesting of brant", was characterized by extensive coverage of snow which gradually melted. The opportunities for foxes to capture prey appeared limited. In the second stage ("brant nesting"), the study area was almost entirely free of snow and most birds which had migrated to the area earlier had started nesting. The date of first nest initiation by brant arbitrarily defined the division between the "pre-nesting" and "nesting" stages. Brant were the most numerous geese, as well as one of the most numerous bird species overall in the Kokechik Bay region, and their nests were vulnerable to fox predation. They served as a visible indication that nesting was underway. We terminated observations very early in the brood-rearing phase of geese, as grass height at this time obscured fox visibility, so I included brood-rearing within the "nesting" stage for analysis.

Table 1. Time periods (A.) and stages (B.) used for analysis and their biological significance for foxes in the study area near Kokechik Bay in 1986. These are general descriptions and not absolute timeframes.

A.

Period	Date	Significance
1	6 May- 18 May	Microtines were the predominant prey of foxes.
2	19 May- 28 May	Foxes recovered egg caches and found the earliest nests of birds other than brant.
3	29 May- 7 June	Initiation of nests by brant and other birds. Peak egg availability to foxes.
4	8 June- 17 June	Incubation in progress for most birds in the study area
5	18 June- 27 June	Late incubation and peak of hatch for brant and other geese.
6	28 June- 7 July	Eggs from late brant nests hatch. Most birds rearing broods.

B.

Stage	Periods	Significance
1	1- 2	"Pre- nesting of brant": most birds had not initiated nests.
2	3- 6	"Nesting of brant": Most nests initiated, and eggs incubated and hatched during this stage. Juvenile birds were available at the end of this stage.

To analyze behavioral variations within each stage on behavior, I divided them into six periods of about 10 days each. I defined periods 1 and 2 (in the "pre-nesting of brant" stage) by the prey base available to foxes and periods 3-6 by the representative goose chronology (Table 1).

I computed descriptive statistics using the SAS statistical package (SAS Institute Inc. 1985a) and tested each distribution for normality using either the Shapiro-Wilk ($n<51$) or the Kolmagorov D ($n>50$) statistic (SAS Institute Inc. 1985a). For all statistical tests, the results were considered significant if a given probability value was <0.05; the degrees of freedom are reported as subscripts in the text.

I hypothesized that the search behavior of foxes might be the most sensitive to changes in available prey, so I tested for differences in search bout duration by period, outcome (successful vs. unsuccessful search bouts), and fox identity. I performed a logarithmic transformation of the data and tested the null hypothesis of no effect of these factors and no interactions among them using a three-way analysis of variance (ANOVA, general linear model) procedure. I used a crossed, fixed effects model with the 3 periods (periods 2, 4, and 5), the two search outcomes, and the four foxes for which I had at least one observation per cell as factor levels (Neter et al. 1985). Foxes were used as a fixed factor because they were not randomly selected from the Kokechik Bay fox population.

An inherent problem in the data was sequential visits to the same nest by a fox until the nest was emptied of all eggs. These subsequent visits could not be considered independent because the fox already knew where the nest was. Accordingly, I calculated the mean duration of each search outcome within an observation session and used these values as the data for the analysis. This was a conservative approach and subject to making a Type II error (Zar 1984). To further analyze interactive trends

suggested by this ANOVA, I repeated the analysis using all individual searches. Interactive effects that became significant in this second analysis were reported, although the analysis was sensitive to making Type I errors.

I computed prey capture rates by dividing the number of items a fox took while under observation by the duration of the observation. I plotted these rates against observation duration to determine the minimum duration of an observation period necessary to accurately estimate capture rates. Observations lasting less than 1000 s (16.7 min) produced poor estimates of rates and were removed from further analyses. I tested for differences between prey capture rates by time period (and stage) using a Kruskal-Wallis (Mann-Whitney) test.

I analyzed the relationship of egg caching to time period and total egg take by foxes using a regression analysis and calculated the differences between slopes of the regression of each period according to Snedecor and Cochran (1976). I also calculated and plotted the mean number of eggs taken from nests and recovered from caches by period to examine the relationship between the availability of fresh eggs and cache retrieval.

Habitat Use

I characterized the habitat use of foxes during the observation periods by vegetation zone and microhabitat, whenever possible. Expanses of snow and mud were considered a type of "microhabitat". If a microhabitat could not be identified it was considered "unknown". I estimated fox "use" of vegetation zones within the study area by the amount of time foxes spent in each zone compared to its availability, based on information supplied by the U.S. Fish and Wildlife Service (Anthony, unpublished data). The proportional use of a zone minus its proportional availability was plotted for individual foxes by the method of Thomas and Taylor (in prep.).

There was no comparable information available on microhabitat composition of each vegetation zone, so I could not estimate microhabitat availability independent of fox activity. I defined an "encounter" of a fox with a microhabitat each time a fox came upon a different microhabitat during its activities. I tested the null hypothesis that fox encounter rates with microhabitats were equal among vegetation zones using the frequency of fox encounters with different microhabitats within vegetation zones with a χ^2 analysis.

To examine the relationship between fox search behavior and habitat use, I analyzed the duration of both successful and unsuccessful seaches in each vegetation zone and microhabitat with a three-way ANOVA (on log-transformed data) with habitat type, search outcome, and the 4 main foxes as fixed factors. I used analyses similar to those described for search behavior by time period.

I calculated the proportion of all search bouts and successful bouts which were conducted in each vegetation zone. I tested the null hypotheses that (1) searches of both outcomes and (2) successful searches were equally distributed among the different vegetation zones using a χ^2 analysis. I tabulated the type of prey which was captured in each vegetation zone and microhabitat type. It was difficult to maintain extensive visual contact with foxes in the high pingo zone in comparison to the other zones. This difficulty resulted in underestimating the time spent in this zone, as well as the frequency of behaviors and prey. This vegetation zone was removed whenever the small sample size would have affected the results of an analysis.

To examine the relationship between fox behavior and habitat use by the period of the summer, I calculated the proportion of time spent in each vegetation zone and microhabitat type, the proportion of search bouts (successful and all searches combined) conducted in the different vegetation zones, and tabulated the type of prey which came from each zone by period.

Den Observations

I and two assistants made observations of active dens only in 1985. In 1986, no active dens were found within the study area due to a lack of reproductive activity by the foxes (Anthony et al. 1987). In July 1985, we observed the dens of 3 pairs for 85 hours in 20 observation periods. We observed the dens from tent blinds (200-300 m from the dens) and 1 observation tower. Observation periods were 5-6 h long between 1900-0100 h (12 periods) and 3 h long between 0600-0900 h (8 periods). We entered the blinds at midday before the observation period and remained until midday the next day to minimize our disturbance to the foxes. We collected information on duration of adult absence from the dens and the type of prey brought to the kits. The difference in duration of absences of male and female foxes was tested using a Mann-Whitney analysis.

Microtine Plots

In 1985 and 1986, the U.S. Fish and Wildlife Service established snaptrap transects at randomly located points in each of the major vegetation zones to obtain an index of microtine population levels in the larger Kokechik Bay study area; in addition, certain transects were sampled for microtine sign (burrows, runways, etc.) in 1986 (Anthony et al. 1985, 1987). To investigate the influence of microtine abundance on fox movements within the observation area, I established 50 m radius plots to sample sign abundance in 1986. These plots were placed at locations of known fox foraging activity in each of the four zones, mapped during the observation periods. Two plots were established in each vegetation zone and in transition areas between the zones for a total of 14 plots. One plot in each zone was

located where a fox had foraged prior to goose nesting; the other plot was located where one foraged during the nesting period. Each plot was sampled once.

In each plot, 18 sampling transects radiated from a center stake at 20° intervals. These transects were divided into 5 m sample units, 1 m wide, which were assigned one score for microtine abundance as each transect was walked. Microtine abundance was scored on the basis of observed runways, burrow holes, and winter nests in the following way: (0) no sign, (1) suspected sign (holes, possible runways), (2) 1-3 runways or a winter nest present, and (3) >3 runways present. Segments dominated by ponds were treated as missing values. I used the proportion of different microtine abundance scores within each microhabitat category to analyze the microtine plot data and tested the null hypothesis that the distribution of sign among microhabitats was equal with a Kruskal-Wallis analysis.

Scats and Prey Remains

Fox scats were collected during both field seasons, while prey remains were collected only in 1985. In 1985, dens known to be active were used as the collection site for both scats and prey remains. Dens were visited irregularly with most visits occurring in July. All scats collected from a den during a visit were pooled in labelled paper bags for drying. The collection of scats from dens late in the season biased the sample toward scats of kits rather than adults. Any prey remains found on the den surface during the visit were put in labelled containers.

As noted earlier, in 1986 no active dens were found within the study area, which precluded regular sampling of scats and collection of prey remains. In April and May, 1986, individual scats estimated to be fresh (<3 d old) and found at such sites as excavated microtine nests, retrieved caches, and exposed mounds were placed

in labelled paper bags. After snowmelt, scats were more difficult to locate. The age of scats collected from captured foxes or recently depredated nests could be determined with some precision, but the age of others could be estimated only generally. In addition to scats, recovered caches and prey remains found opportunistically in 1986 were brought back to camp and identified. No distinction could be made between prey scavenged or killed by foxes using this method.

Prey remains from 1985 were identified using the reference collection and with help from the staff of the University of Alaska Fairbanks museum. Scats were autoclaved to prevent my exposure to the eggs of the tapeworm, Echinococcus multilocularis, and examined with a dissecting microscope to identify remains. The 1985 scats were classified simply by presence or absence of mammal and bird remains. No frequency of occurrence calculations were possible because individual scats had been mixed together during collection. In 1986, remains found in the scats were identified to the lowest taxon possible and the proportion of scats containing different prey types was calculated. Other methods for calculating the contribution of different prey types to the diet (Lockie 1959) would have seriously underestimated the contribution of eggs to the diet of foxes. I observed that eggs leave little undigestible material in the scats; eggshell fragments are ingested incidentally, if at all.

For analysis of the scats, I considered the six time periods defined in Table 1 and two additional periods. Period 0 consisted of all scats collected before observations were started and period 7 of those collected after observations were terminated in July. The proportion of scats that contained remains of different prey types was plotted against the period of the summer and a Spearman rank correlation coefficient was calculated for the relationship between prey type and time period.

RESULTS

During the two years of the study, 11 foxes were known to have ranges which at least partially overlapped the observation area. Foxes in the study area generally foraged alone, although members of a pair occasionally hunted together.

In 1985, four foxes were seen, two regularly. One pair of foxes raised kits, the other two foxes were paired, but had no kits. These foxes were observed 26 times ($\bar{X}$=31.0 min, range=1-215 min) for a total of 19 h. The foxes with kits returned periodically to their den which may have limited their possible foraging time in distant habitats. In July 1985 (after weaning), fox absences from dens averaged 99 min (range=4-203, n=23 trips). There was no difference between males and females in the duration of absence (Mann-Whitney $U_{16,7}$=184.5, $P > 0.05$). No data at dens were collected during the nursing period (ca. mid May-mid June).

In 1986, seven foxes were seen, of which four were observed on a regular basis. For undetermined reasons, none of the foxes in 1986 raised kits (Anthony et al. 1987). The foxes most frequently observed in the study area included Fox 1 (a male) and Fox 2 (a female), a pair with home ranges largely inland from the coast (Anthony et al. 1987; Appendix A). A female seen in 1985 (Fox 3) returned in 1986 to her coastal range to the north of Foxes 1 and 2 (Anthony et al. 1987; Appendix A). Fox 3 was paired with Fox 5 until early June, when she formed a bond with Fox 4. After late May, the range of Fox 5 was largely west of the study area.

Foxes 3 and 4 expanded their range inland after the death of Fox 1 in early July (Anthony et al. 1987). Foxes 6 and 7 (both males) were probably siblings (Anthony et al. 1987); most of their range was east of the study area. In 1986, we had 140 sightings of foxes ($\bar{X}$=46.6 min, range=1-215 min), totailing approximately 95 h.

The Influence of Time Period and Habitat on Foraging Behavior

Seasonal Patterns in Search and Movement Behavior

The percentage of search bouts that were successful was lowest during the pre-nesting stage (periods 1-2), highest in period 3 when brant incubation had begun, then gradually declined throughout the remainder of the summer (Fig. 3). Search bouts conducted by foxes in periods 1-2 were of longer duration than those initiated in periods 3-6 (brant nesting stage) (Period effect, Table 2; Fig. 4, Fig. 5). Successful search bouts tended to be shorter than unsuccessful searches (Success effect, Table 2; Fig. 4, Fig. 5). Individual foxes did not differ significantly in their search patterns over time.

The duration of travel bouts was longest in period 1 when much of the study area was covered by snow, and foxes travelled from one exposed area to the next. The duration of travel bouts started to decline during snowmelt (in period 2) and continued to decline throughout the remainder of the summer (Fig. 6).

General Use of Habitats by Arctic Foxes

The amount of time foxes were observed in each vegetation zone was disproportionate to its availability in the study area (Table 3). Proportionately more time was spent by foxes in low pingo (23%) and short sedge meadow (35%) than expected, given the availability of these two zones. In contrast, we observed

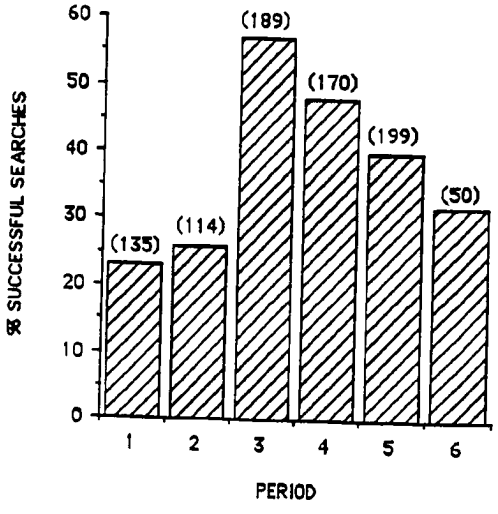

Fig. 3. The proportion of successful search bouts of arctic foxes by time period in the study area near Kokechik Bay, 1986. Sample sizes (no. of search bouts) indicated in parentheses.

Table 2. Three-way analysis of variance of the effects of time period, search outcome, and fox on the log of mean duration of search bouts within observation sessions of arctic foxes in the study area near Kokechik Bay, 1986. The analysis included four foxes (Foxes 1-4) during three periods (2, 4, and 5).

Source	df	MS	F	P
Period	2	2.93	3.98	0.025
Success	1	6.26	8.46	0.006
Fox	3	0.24	0.33	0.803
Period*Success	2	0.84	1.13	0.333
Period*Fox	6	0.47	0.64	0.700
Success*Fox	3	0.61	0.82	0.490
Period*Success*Fox	6	1.29	1.74	0.134
Error	45	0.74		

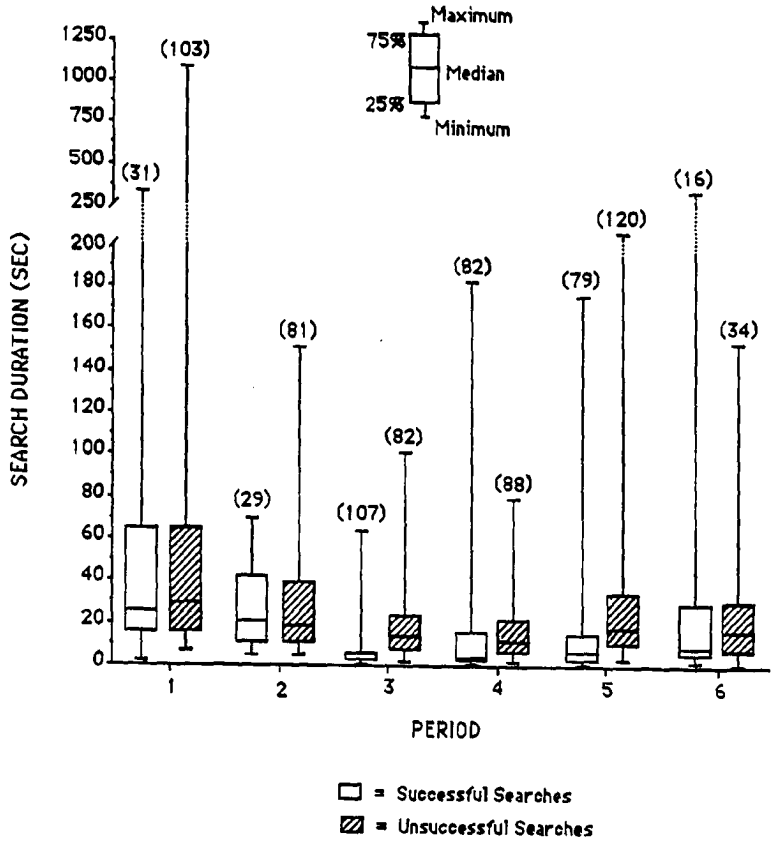

Fig. 4. The duration of successful and unsuccessful searches of all arctic foxes by period in the study area near Kokechik Bay for the summer of 1986. Sample sizes (no. of searches) are indicated in parentheses.

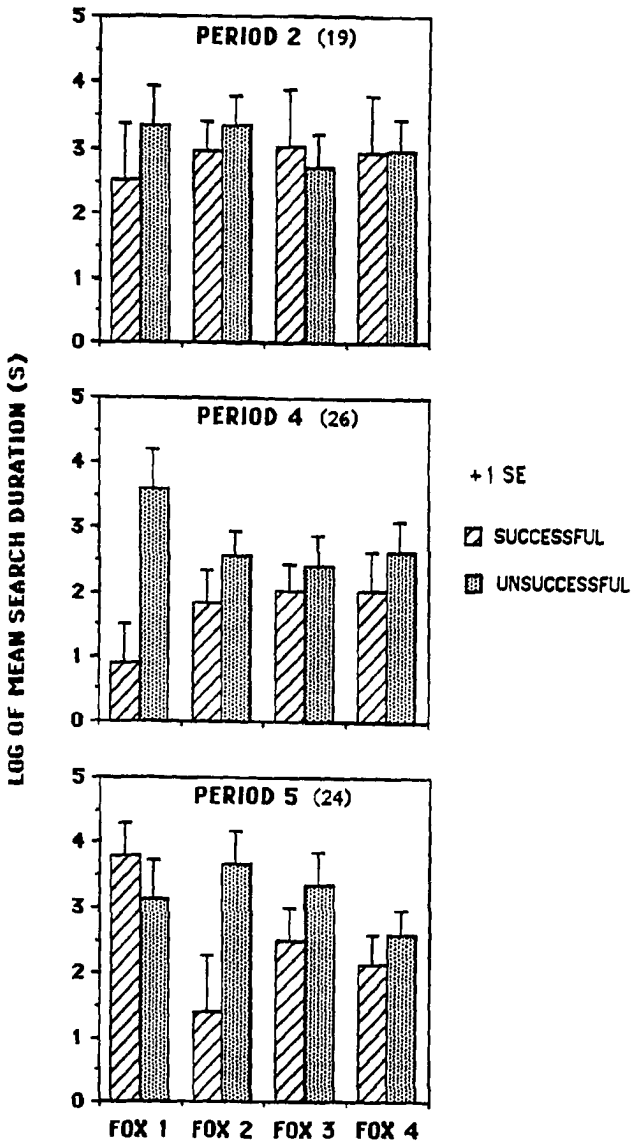

Fig. 5. The mean duration of search bouts within observation sessions of individual arctic foxes by period in the study area near Kokechik Bay, Alaska in 1986. The standard error for each value and the sample size of observation sessions for the period are indicated.

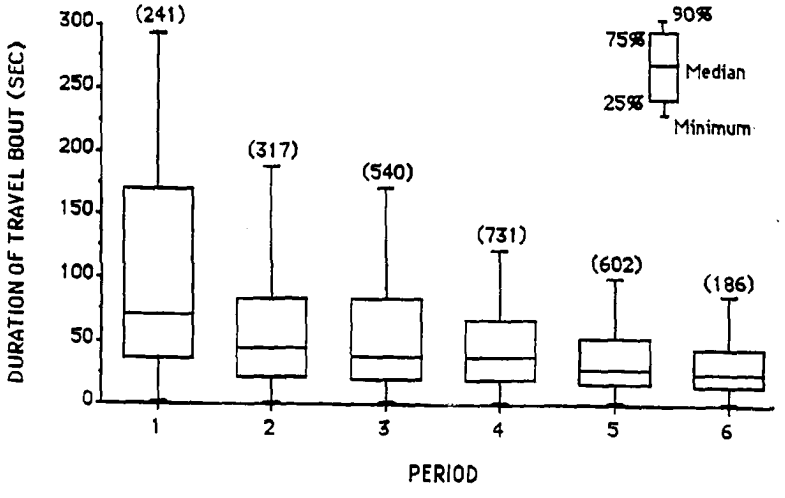

Fig. 6. The duration of travel bouts of arctic foxes by time period of the summer in the study area near Kokechik Bay, Alaska in 1986. Quantiles and sample sizes indicated in figure.

Table 3. The availability of different vegetation zones within the study area near Kokechik Bay, Alaska in 1986. The proportion of time that arctic foxes were observed and the proportion of successful search bouts in each zone are also represented.

Vegetation Zone Type	Availability Within the Study Area (%)	% Fox Use	% Successful Searches
Short Sedge Meadow	24	35	45
Grass-Sedge Meadow	41	37	23
Low Pingo	16	23	44
High Pingo	13	5	9

foxes for less time (5%) than expected in the high pingo zone. Individual foxes differed in their use of vegetation zones (Fig. 7); habitat use depended on range location (Anthony et al. 1987; Appendix A) and temporal avoidance of neighbors in overlap areas. Foxes 1 and 2 spent a greater percentage of time in the low pingo zone, and less in the grass-sedge meadow zone, while Foxes 3 and 4 spent more time in the short sedge meadow habitat, and less in the two pingo habitats. We observed Foxes 5-7 most of the time in the grass-sedge meadow while they were in the study area.

The encounter rates of foxes with the different microhabitats was not equal among vegetation zones (χ^2_6=602.2, P < 0.001; Table 4). Fox activities coincided most with grass meadows in all zones except the high pingo zone, where encounters with pingos predominated.

Patterns of Search Behavior among Habitats

Foxes conducted comparable numbers of search bouts in the short sedge meadow (38%), the grass-sedge meadow (33%), and low pingo (27%) zones (χ^2_2=1.79, P > 0.05, n=857 searches; Fig. 8). Few searches (1%) were observed in the high pingo zone. Searches conducted in the short sedge meadow and low pingo zones had a higher probability of success than did those conducted in the grass sedge meadow (χ^2_3=16.67, P < 0.001; Fig. 9). Searches in the high pingo zone had a low success rate (9%).

The duration of search bouts did not differ significantly among vegetation zones (Table 5; excluding the high pingo zone). Individual foxes differed in their search patterns with Fox 1 conducting searches of longer duration than foxes 3 and 4 (Fox effect; Table 5; Fig. 10). When individual searches were considered in the analysis, the interaction between zones and foxes, and between zones, foxes, and search outcome suggested by the previous analysis became significant ($F_{6,743}$=4.76, P < 0.001 and

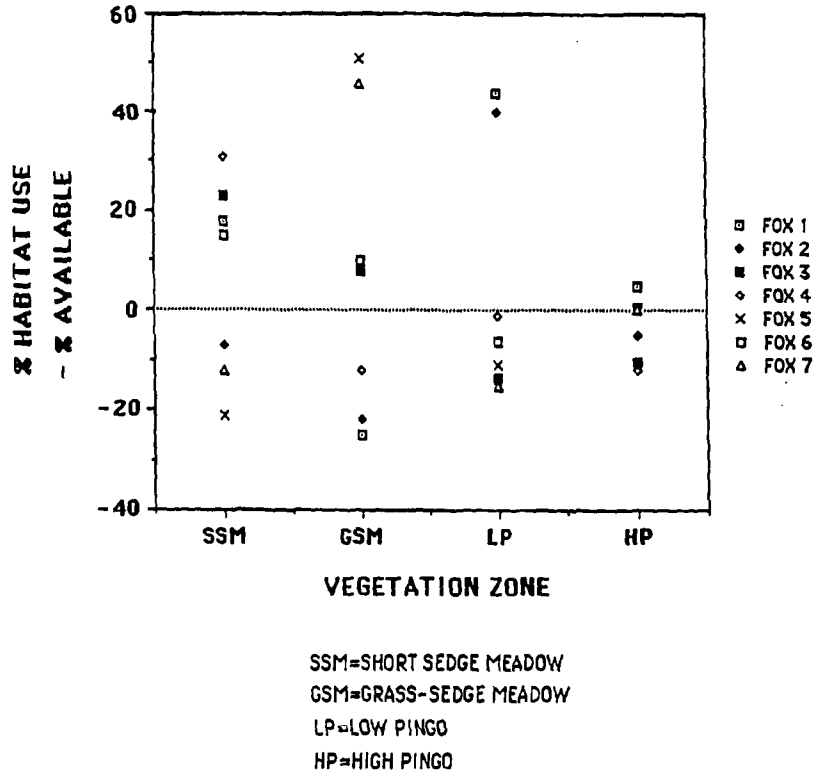

Fig. 7. The proportional time spent in the different vegetation zones by individual foxes minus the proportional availability of each zone in the study area near Kokechik Bay, Alaska in 1986.

Table 4. The frequency of encounters of arctic fox activities with different microhabitats within each vegetation zone in the study area near Kokechik Bay, Alaska in 1986. The proportion of encounters of microhabitats within each vegetation zone is included.

Vegetation Zone	Grass Meadow n (%)[a]	Shore n (%)	Pingo n (%)	Total
Short Sedge Meadow	936 (74)	302 (24)	28 (2)	1266
Grass-Sedge Meadow	694 (50)	460 (33)	244 (17)	1398
Low Pingo	529 (54)	208 (21)	242 (25)	979
High Pingo	21 (19)	7 (6)	84 (75)	112
Total	**2180 (58)**	**977 (26)**	**598 (16)**	**3755**

a. Row Percent

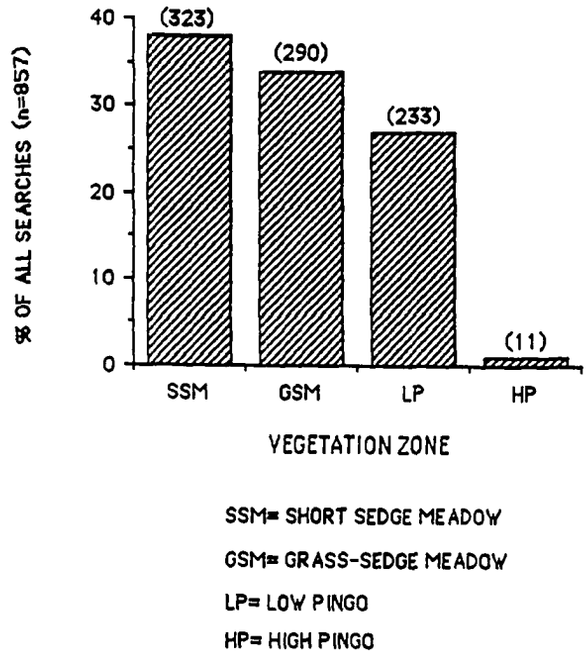

Fig. 8. The percent of all searches conducted by arctic foxes near Kokechik Bay that occurred in the different vegetation zones within the 1986 study area. Sample sizes indicate the number of search bouts conducted in each vegetation zone.

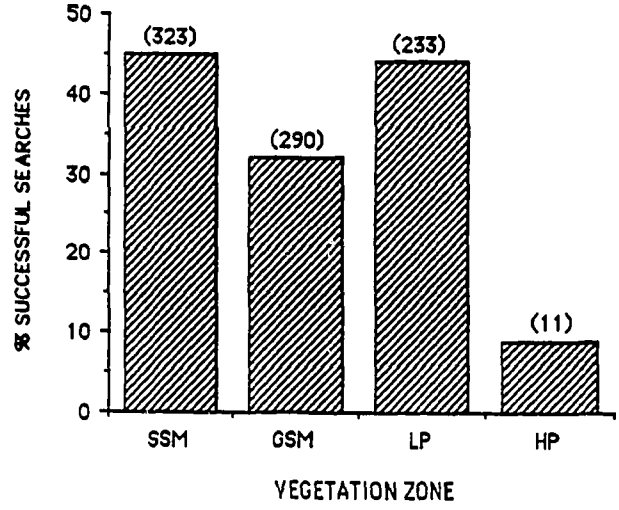

Fig. 9. The percent of successful searches within each vegetation zone of arctic foxes in the study area near Kokechik Bay, 1986. Sample sizes indicate the number of search bouts counted in each zone.

Table 5. Three-way analysis of variance of the effects of vegetation zone, search outcome, and fox identity on the log of mean search duration within observation sessions of arctic foxes in the study area near Kokechik Bay, 1986. The analysis included four foxes (Foxes 1-4) and three vegetation zones (short sedge meadow, grass-sedge meadow, and low pingo).

Source	df	MS	F	P
Vegetation Zone	2	1.55	1.83	0.165
Success	1	0.30	0.35	0.553
Fox	3	4.34	5.10	0.002
Zone*Success	2	1.61	1.89	0.156
Zone*Fox	6	1.39	1.64	0.142
Success*Fox	3	0.69	0.81	0.493
Zone*Success*Fox	6	1.39	1.61	0.148
Error	128	0.85		

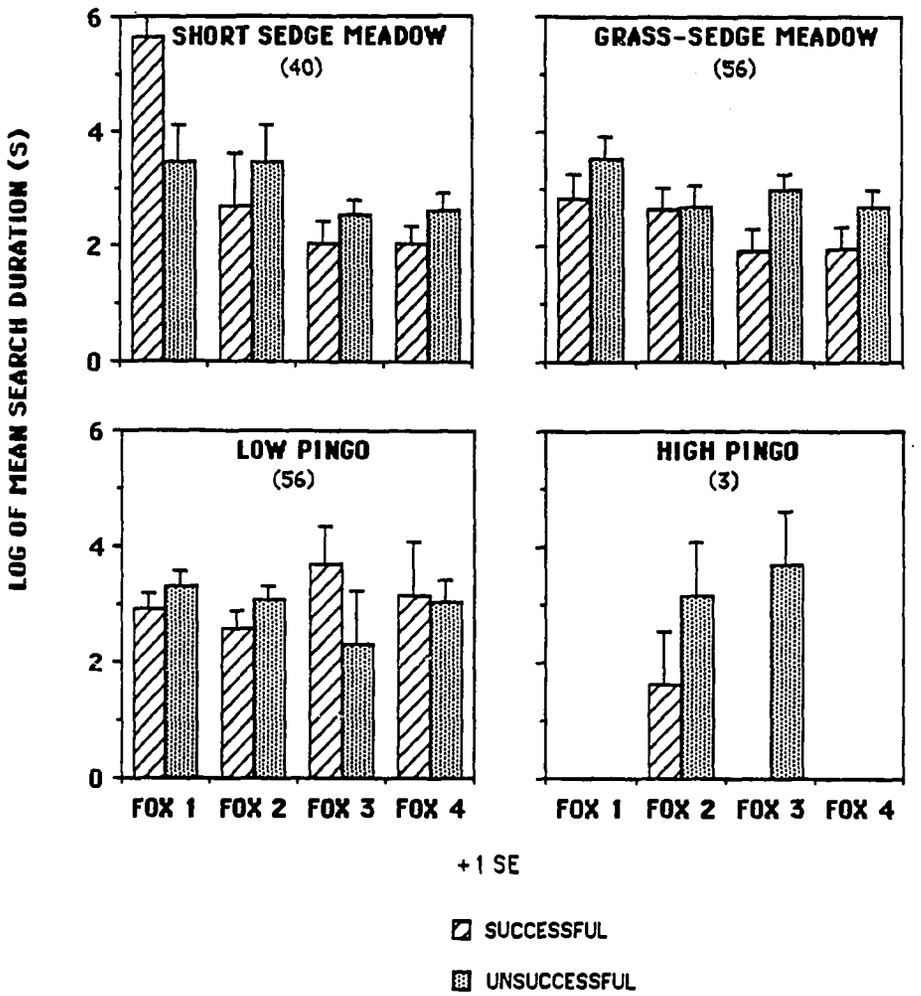

Fig. 10. The mean duration of search bouts within observation sessions of individual arctic foxes in the vegetation zones in the study area near Kokechik Bay, Alaska in 1986. The standard error for each value and the sample size of observation sessions for each vegetation zone are indicated.

$F_{6,743}=3.60$, P=0.002, respectively). Fox 1 conducted his shortest searches in the low pingo zone and his longest searches in the short sedge meadow. In contrast, the searches of Foxes 3 and 4 were shortest in the meadow zones and longest in the low pingo zone. Individual foxes also differed in their patterns of successful and unsuccessful search duration among zones (Fig. 10).

Search bout duration did not differ significantly among the microhabitats used by foxes, although search bouts conducted in grass meadows were somewhat shorter than those conducted on pingos (Table 6; Fig. 11). There were significantly different patterns among foxes (Fox effect) and between successful and unsuccessful search bouts (Success effect; Table 6; Fig. 11).

Habitat Use by Time Period

The proportion of time that foxes were observed in each vegetation zone in the study area differed among periods (Fig. 12). Time spent in the short sedge meadow peaked in period 3 (clutch initiation/early incubation of brant) and subsequently declined, while time in the grass-sedge meadow peaked in period 4. Foxes spent more time in the high pingo zone in period 1 (microtine period) and period 6 (late hatch/brood-rearing) than during the intervening periods.

The proportion of time foxes were observed using the different microhabitats also differed among periods (Fig. 13). The time spent on pingos was greatest in periods 1-2, while time spent in grass meadows was greatest during the nesting stage (periods 3-6).

The Effect of Time Period and Habitat on Search Behavior

In period 1, foxes conducted a similar number of searches in all vegetation

Table 6. Three-way analysis of variance of the effect of microhabitat, search outcome, and fox identity on the log of mean duration of search bouts within observation sessions of arctic foxes near Kokechik Bay, 1986. The analysis included three foxes (Foxes 1, 2, and 4), and three microhabitats (grass meadows, shores, and pingos).

Source	df	MS	F	P
Microhabitat	2	0.19	0.20	0.822
Success	1	5.32	5.54	0.020
Fox	2	5.11	5.32	0.006
Micro*Success	2	0.44	0.46	0.630
Micro*Fox	4	0.99	1.03	0.394
Success*Fox	2	1.30	1.35	0.263
Micro*Success*Fox	4	0.92	0.96	0.432
Error	127	0.96		

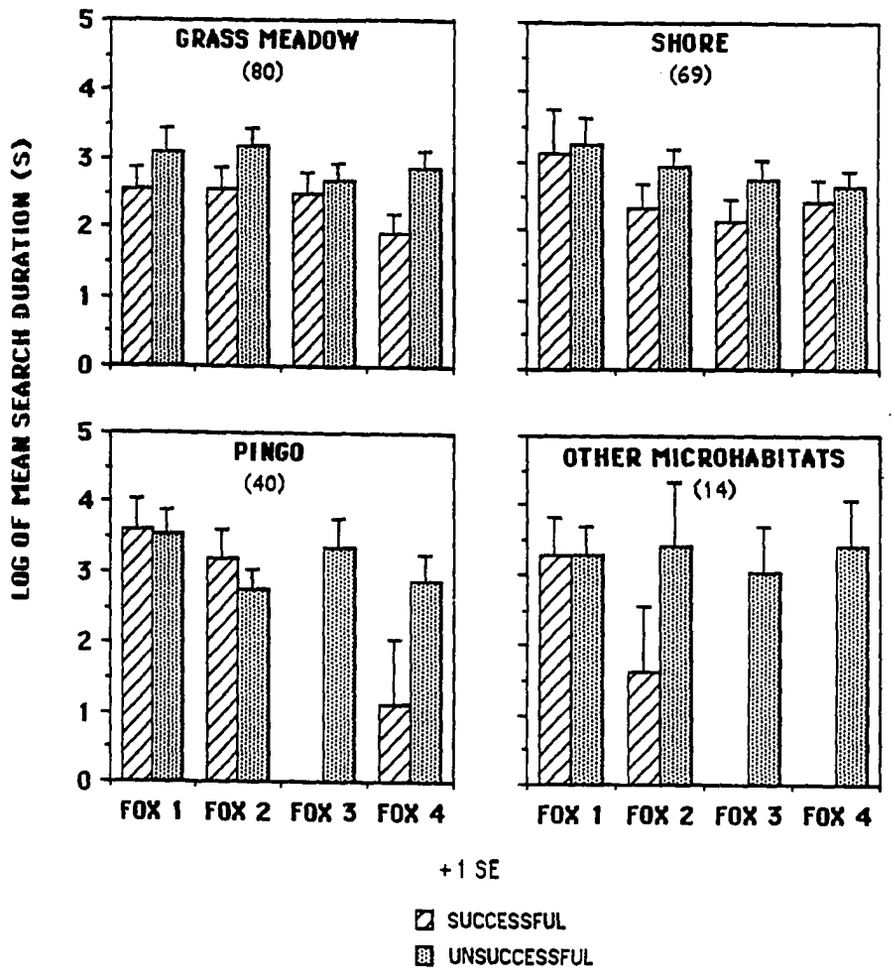

Fig. 11. The mean duration of search bouts within observation sessions of individual arctic foxes in the different microhabitats in the study area near Kokechik Bay, Alaska in 1986. "Other" microhabitats included snow and mud. The standard error for each value and the sample size of observation sessions for each microhabitat are indicated.

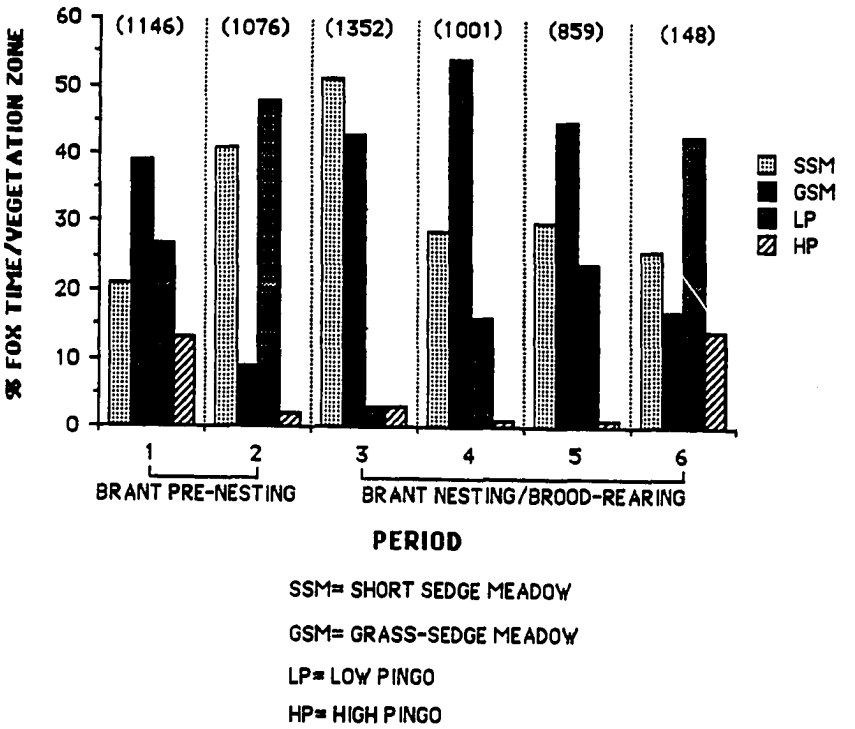

Fig. 12. The proportion of time which arctic foxes spent in the various vegetation zones by period within the 1986 study area near Kokechik Bay, Alaska. Sample sizes indicate the total time (min) foxes were observed in each period.

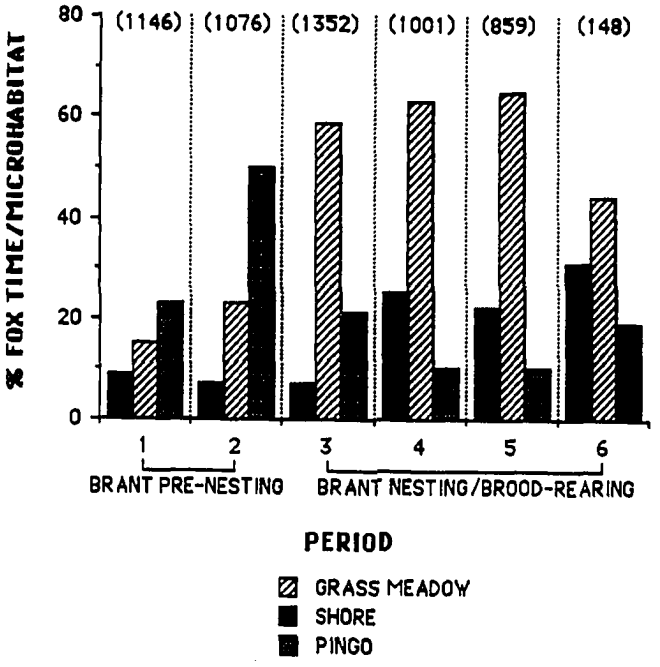

Fig. 13. The proportion of time which foxes spent in various microhabitats within the study area near Kokechik Bay, Alaska in 1986. Sample sizes are the number of minutes foxes were observed during each period.

zones except the high pingos (Fig. 14). Proportionately more searches were conducted in the short sedge meadow in periods 2-3, with a subsequent decline in periods 4-6 as search effort shifted first toward the grass-sedge meadow and then the low pingo zones (χ^2_{10}=146.46, P < 0.001; Fig. 14). Very few searches were observed in the high pingo zone during the summer.

Despite a decline in the proportion of searches conducted in the short sedge meadow zone during period 4 (Fig. 14), success there remained high (Fig. 15). Search duration was similar in period 4 to that of period 3 ($\bar{X}$=3.9 s, compared to $\bar{X}$=5.2 s in period 3) ($F_{1,147}$=0.97, P=0.33), indicating that search frequency in this zone was positively related to the number of bird nests encountered, not an increase in search duration. In period 4, searches in the grass-sedge meadow accounted for 55% of the total (n=170 searches; Fig. 14); fewer than half (41%, n=93 searches; Fig. 15) of these were successful. In period 5, the high percentage of successful searches in the low pingo zone (59%, n=77 searches) was related to the total depredation of a small brant colony.

Prey Capture by Time Period and Habitat

Seasonal Patterns in Prey Capture Rates

The overall median capture rate of prey for the summer was 2.7 items/h (n=67 observations and 385 items). Capture rates for the six periods of the summer ranged from a median of 1.5 items/h in period 1 to 5.3 items/h in period 6 (Fig. 16). Periods 1 and 2 did not differ from each other (Kruskal-Wallis χ^2_1=0.06, P=0.81), nor was there significant variation among periods 3-6 (Kruskal-Wallis χ^2_3=2.5, P=0.48). Therefore, I pooled data into two groups representing the pre-nesting and nesting stages of brant. Foxes achieved greater capture rates in the

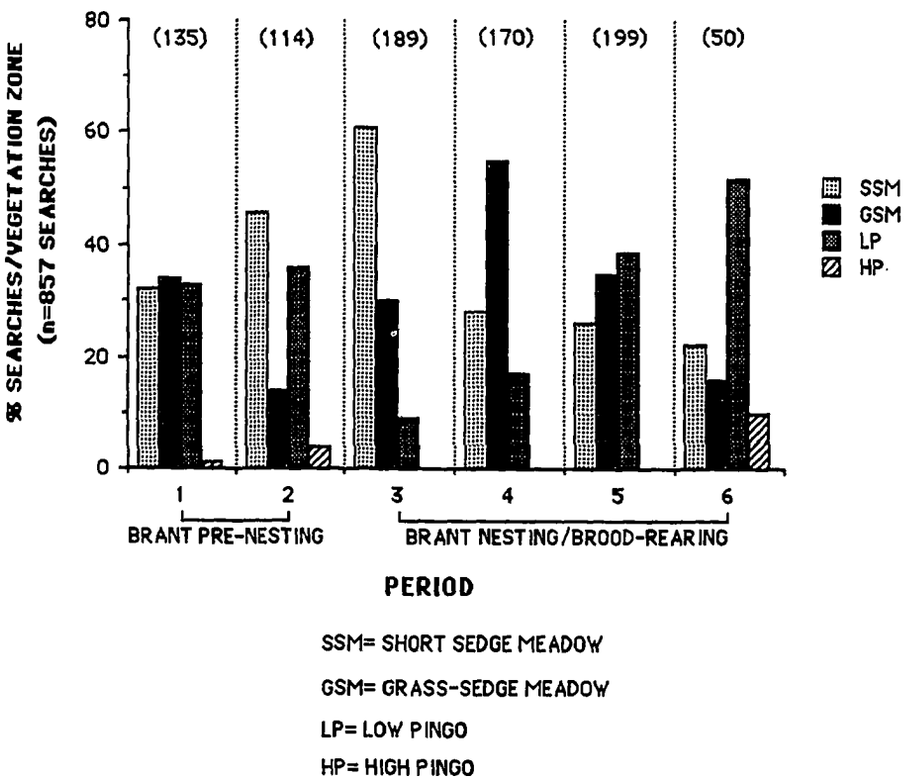

Fig. 14. The proportion of search bouts initiated by arctic foxes in each vegetation zone by period within the 1986 study area near Kokechik Bay, Alaska. Sample sizes indicate the number of search bouts which were observed in each period.

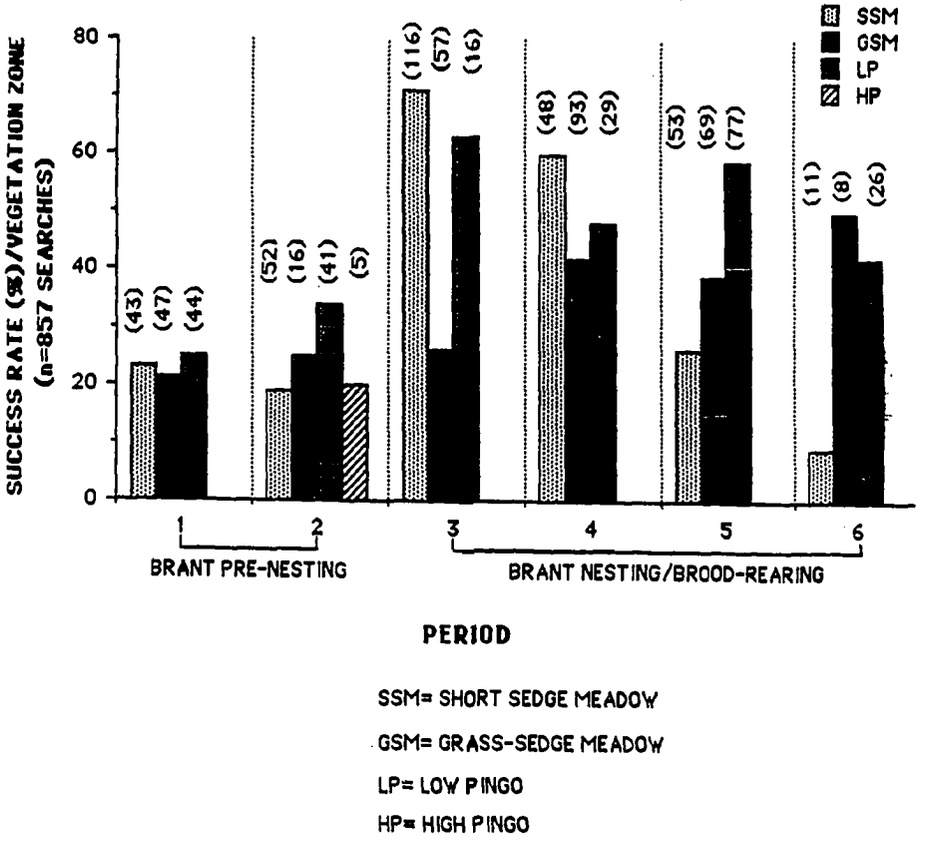

Fig. 15. The proportion of successful search bouts conducted by foxes in different vegetation zones in the study area near Kokechik Bay, Alaska in 1986. Sample sizes indicate the number of search bouts conducted in each vegetation zone by period.

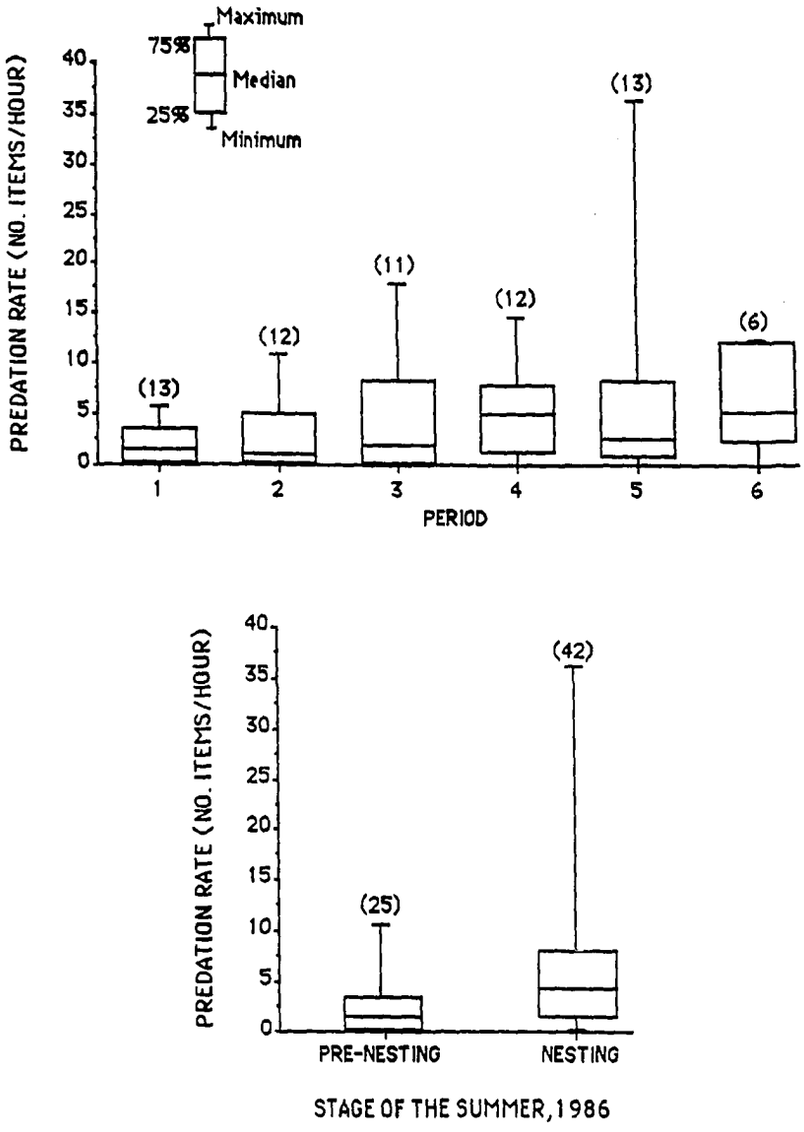

Fig. 16. Prey capture rates of arctic foxes in the study area near Kokechik Bay by period (above) and stage (below) of the summer, 1986. Sample sizes are based on observations of foxes that lasted longer than 16 minutes.

nesting stage than in the pre-nesting stage (median=3.8 versus 1.1 items/h; Kruskal-Wallis $\chi^2_1=6.15$, P=0.01; Fig. 16).

We observed foxes taking 312 eggs (of geese, gulls, loons, ducks, and shorebirds); 98% of these were taken in periods 3-6. The median egg capture rate for periods 3-6 was 3.5 eggs/h (range=0-36.3 eggs/h, *n*=42 observations; Fig. 17). This is similar to the total capture rate (3.8 items/h) because eggs were the primary prey of foxes during the nesting stage. The variation in egg capture rates among periods 3-6 was not significant (Kruskal-Wallis $\chi^2_3=1.48$, P=0.69).

Foxes cached at least 80% of all eggs taken (the fate of some eggs taken by foxes was not observed). At least 89% of eggs taken in period 3 were cached, 82% in period 4, 72% in period 5, and 53% in period 6. There was a linear relationship between the number of eggs that foxes cached and the number of eggs that they took (Fig. 18). The negative intercept of each regression (Fig. 18) suggests that foxes met their maintenance needs even though they cached most eggs that they encountered. The proportion of cached eggs differed among periods ($F_{6,35}=5.36$, P<0.001).

We saw foxes eat few eggs when they encountered nests during the summer (14% of all eggs taken). In periods 3-4, only 8% of the eggs taken were eaten, increasing to 23% and 37% in periods 5 and 6, respectively. Because foxes usually consumed eggs at nests or caches, these are minimum estimates. Foxes might eat all the eggs in a particular nest or only a portion, caching the rest. Eggs were not eaten each time a nest was encountered, but eggs were cached from most nests that foxes located.

When foxes cached eggs, they removed them singly, carried them 5-400 m away, and buried them separately. A fox returned to the same nest to empty it, making a final visit after the nest was already empty. If a fox encountered a new nest while carrying an egg (only likely to occur in a high density brant nesting area), the

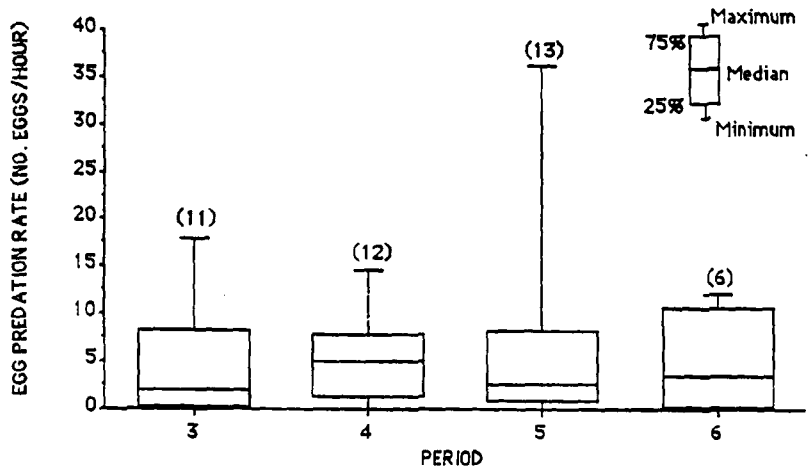

Fig. 17. Egg capture rates of arctic foxes in the study area near Kokechik Bay, 1986. Only the periods during the nesting stage are shown. Sample sizes represent number of observation sessions.

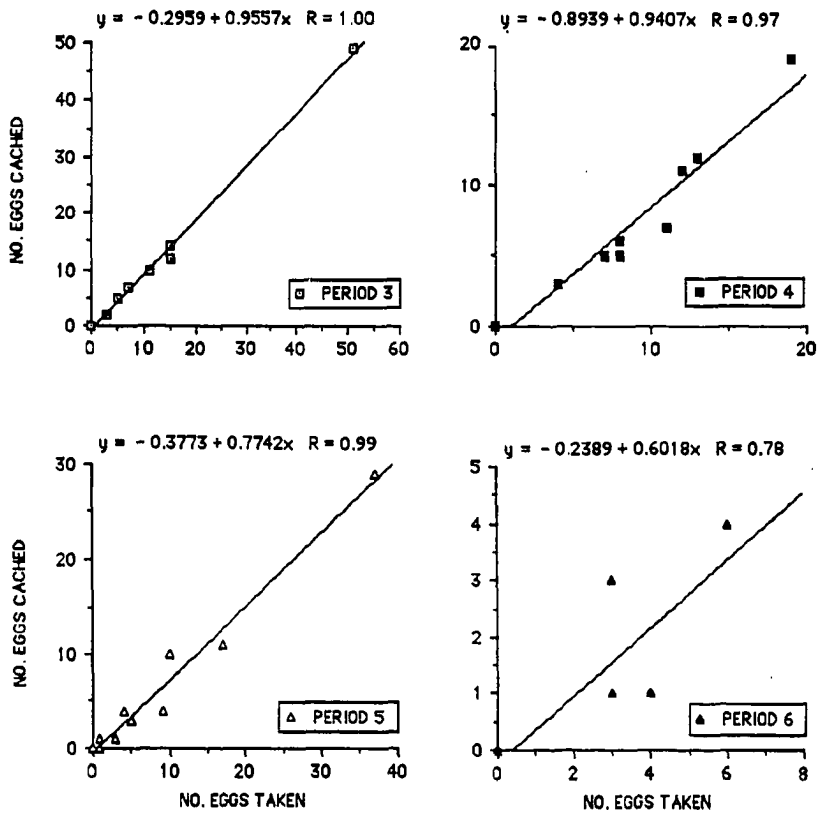

Fig. 18. The relationship between the number of eggs known to be cached and the number of eggs taken by arctic foxes in the study area near Kokechik Bay during the summer of 1986. Data points represent observation sessions.

fox seemed confronted by two conflicting stimuli: (1) to bury the egg it was carrying, or (2) to take eggs from the new nest. We twice saw a fox drop and leave the egg it was carrying when it encountered a new nest.

Foxes in the study area appeared to skirt high density nesting aggregations of brant, preying mainly upon the nests on the periphery. In the case of a group of 67 nests on a peninsula, two female foxes made visits early in incubation, but only took eggs from nests on the outskirts. This behavior was consistent with fox activity we observed around other high density aggregations. However, immediately prior to hatch, one male fox made two visits to the peninsula colony in 1.5 h, in which he penetrated the interior and took at least 37 eggs, resulting in the final destruction of the colony.

As the number of active nests declined, the retrieval of eggs from caches increased. Foxes retrieved eggs from caches on 6 occasions in periods 5-6, but no retrievals were observed during periods 3-4 (Fig. 19). Recovery rates differed significantly among periods ($F_{5,41}=7.15$, $P=0.01$), with a maximum rate of 3.58 eggs/h achieved in period 6. We observed foxes retrieve at least 1 egg from an overwintered cache in period 1 and 2 eggs in period 2. This is a low estimate of egg cache recovery for period 2 because we found at least 15 overwintered caches that were recovered by foxes within 200 m of camp during this time. A limited number of fresh eggs (from birds other than brant) became available to foxes during this period.

Additional Information on Fox Diets

Food remains in fox scats indicated changes in diet as prey availability changed. In 1985, 10 scats collected in May contained only mammalian remains [fox

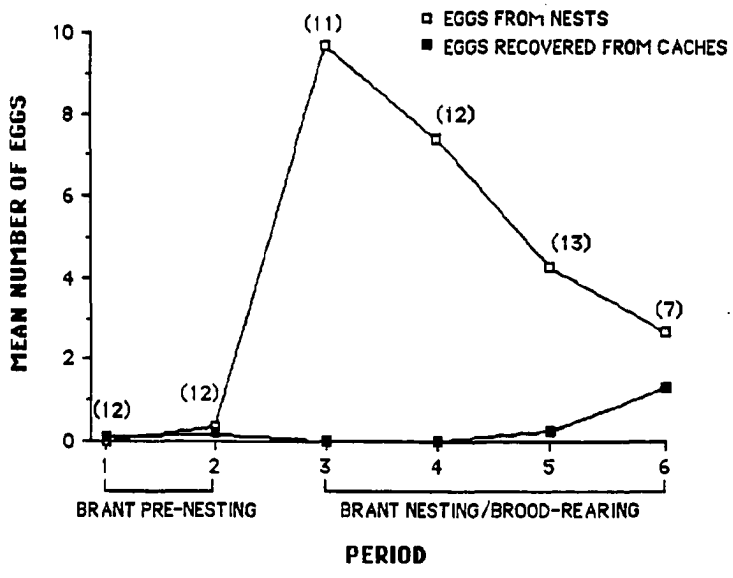

Fig. 19. The mean number of eggs recovered from caches during the summer relative to the mean number of eggs taken from nests by arctic foxes by period in the study area near Kokechik Bay, Alaska in 1986. Both values in period 5 excluded the observation session when one fox destroyed a small brant colony just prior to hatch. Sample sizes indicate the number of observation sessions greater than 16 min in duration.

and muskrat (Ondatra zibethica) hair, microtine teeth and hair]. The 98 scats collected in July and August contained primarily bird bones, down, feathers and egg shells, but 18% contained some mammalian remains. The age of these scats could not be determined precisely. In 1986, the proportion of scats with small mammal remains (predominantly Microtus oeconomus) declined through the summer (Spearman's rho=-0.95, P<0.001, n=96), while the proportion with egg remains increased (Spearman's rho=0.74, P=0.037, n=96) (Fig. 20). There was no apparent relationship between presence of bird remains or other components (fox fur, vegetation, etc.) and time. The age of 38% of all scats with small mammal remains (n=61) and 58% of those collected in periods 3-6 (n=19) could not be determined precisely; some of these scats may have been from earlier periods.

We collected 23 prey remains from the surface of dens in 9 visits in 1985. Small mammals (n=2) were the only prey found at dens in May (Appendix B). Of the remains collected in June-August, bird remains represented 76% (n=16) while eggs represented 19% and small mammals 5%.

We observed adult foxes returning with prey on 13 occasions during den observations in the brood-rearing period of July 1985 (Appendix C). Nine birds (69%) of different species were brought to the dens, of which 56% were goslings. Two eggs (13%) were also brought, one of these came from a cache near the den.

Prey Captures by Habitat

Counts of successful prey captures differed among the vegetation zones (Table 7). Half of the eight confirmed small mammal captures came from the short sedge meadow zone. We did not observe foxes capture any small mammals in the high pingo zone. We observed foxes eat two birds (1 adult and 1 gosling cackling Canada goose) and both incidents were in the grass sedge meadow. Over 40% of all eggs taken

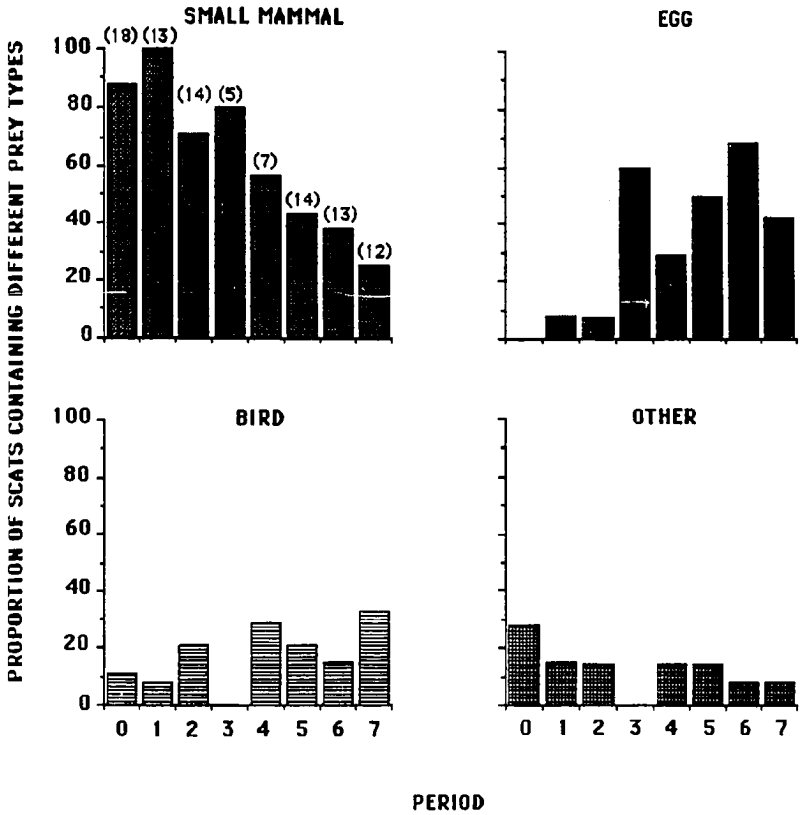

Fig. 20. The contents of arctic fox scats (N=96) collected during the summer of 1986 near Kokechik Bay, Alaska. Period 0 included scats collected before observations of fox behavior began and period 7 those collected after observations ended. Sample sizes (no. of scats) for each period indicated.

Table 7. The number of prey caught or recovered by arctic foxes by microhabitat within each vegetation zone in the study area near Kokechik Bay, 1986.

Vegetation Zone	Microhabitat	Prey Type: Small Mammal	Egg	Bird	Unknown	Totals
Short Sedge Meadow	Grass Meadow	2	101	0	5	108
	Shore	1	24	0	7	32
	Pingo	0	2	0	0	2
	Other	1	0	0	0	1
	Unknown	0	3	0	3	6
Grass-Sedge Meadow	Grass Meadow	0	43	1	2	46
	Shore	1	39	0	2	42
	Pingo	1	11	0	2	14
	Other	0	0	1	3	4
	Unknown	0	5	0	0	5
Low Pingo	Grass Meadow	0	58	0	14	72
	Shore	0	16	0	9	25
	Pingo	1	8	0	10	19
	Other	1	0	0	0	1
High Pingo	Grass Meadow	0	0	0	1	1
	Pingo	0	2	0	0	2
	Totals	**8**	**312**	**2**	**63**	**385**

by foxes were from the short sedge meadow (24% of the overall habitat), while 31% and 26% were taken from grass-sedge meadow and low pingo zones (41% and 13 % of the overall habitat, respectively). Few eggs (1%) were from the high pingo habitat and these were eggs recovered from caches.

Capture of prey also differed among microhabitats among vegetation zones. Most eggs (65%) were taken by foxes from grass meadow microhabitats; 33% came from grass meadows within the short sedge meadow zone (Table 7). We observed foxes capture small mammals in all microhabitat types.

Prey Captures by Time Period and Habitat

Prey captured by foxes varied with time and habitat (Table 8). All confirmed small mammal captures occurred during the pre-nesting stage. We observed foxes take seven eggs during this time; three (spp. unknown) were recovered from caches, but four came from nests of other geese which initiated nesting before brant. A fox ate and cached portions of an adult cackling Canada goose during the pre-nesting stage; the cause of death was unknown.

Eggs were the main prey of foxes during the nesting stage and most were from the short sedge meadow. Although the exact proportion was unknown, most eggs (over 50%) taken were those of geese, particularly brant. I observed a fox take one gosling during brood-rearing. We did not observe foxes capture any small mammals during the nesting stage, although analysis of the scats (Fig. 20) indicated that some predation of microtines still occurred.

Microtine Sign and Habitat

Data from the microtine sign plots sampled in 1986 indicated that the observed small mammal captures by foxes were not representative of the summer

densities of this prey type among habitats. Microtine sign was abundant and significantly higher along the sides of pingos than in grass meadow, shore or pingo top microhabitats (Kruskal-Wallis $X^2_3=203.1$, $P<0.05$; Fig. 21). None of the sign observed during sampling was fresh, which suggested that microtine populations had declined sometime between late May and when the plots were sampled in July.

Table 8. The number of prey that arctic foxes captured within each vegetation zone in the study area near Kokechik Bay, Alaska in the pre-nesting and nesting stages of brant in 1986. The egg category refers to all eggs taken by arctic foxes, not just those of geese.

	Vegetation Zones									
	SSM[a]		GSM[b]		LP[c]		HP[d]		Totals	
Prey Type	Pre-Nest	Nest	Pre-Nest	Nest	Pre-Nest	Nest	Pre-Nest	Nest	Pre-Nest	Nest
Small Mammals	4	0	2	0	2	0	0	0	8	0
Eggs	0	130	3	95	2	80	2	0	7	305
Birds	0	0	1	1	0	0	0	0	1	1
Unknown	17	2	6	3	23	11	0	1	46	17
Totals	21	132	11	98	26	91	2	1	62	323

a. SSM=Short sedge meadow
b. GSM=Grass-sedge meadow
c. LP=Low pingo
d. HP=High pingo

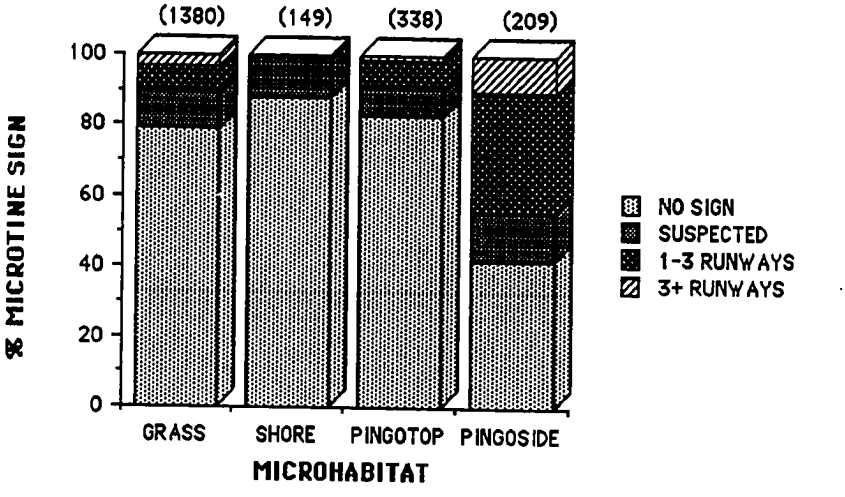

Fig. 21. The proportion of each microhabitat in the study area near Kokechik Bay, Alaska in 1986 that had different categories of microtine sign. Sample sizes are the frequency of occurrence of each microhabitat within the microtine sign sampling plots.

DISCUSSION

The Dynamics of Prey Availability near Kokechik Bay

Seasonal prey availability, and its abundance and distribution throughout the different vegetation zones in the study area near Kokechik Bay, influenced the foraging behavior, diet, and habitat use by arctic foxes. Small mammals (microtines) dominated the diet of arctic foxes in the late spring, but as birds initiated nests, their eggs became the primary prey.

The duration of search bouts conducted by foxes reflected changing prey availability. During the nesting stage of brant near Kokechik Bay, foxes were more successful (Fig. 3) and spent less time searching than in the pre-nesting stage (Fig. 4), because eggs were abundant and acquired relatively easily once a nest was located. As a result, the duration of successful search bouts declined dramatically. Foxes also terminated unsuccessful search bouts sooner in the nesting stage, in response to the increased abundance of prey.

The foraging patterns of foxes were further influenced by prey availability in the vegetation zones within their ranges, which in turn, was probably influenced by the availability of microhabitats within the vegetation zones. Fox activities had a higher probability of taking place on mounds and pingos in the pingo vegetation zones compared to the meadow zones (Table 4). Prey species foxes encountered in pingo microhabitats were white-fronted and emperor geese, as well as other birds with

dispersed nesting patterns (Holmes and Black 1973, Mickelson 1975, Ely and Raveling 1984), and microtines. These geese were capable of defending their nests against foxes, and the subterranean habits of the microtines, in addition to their low densities in 1986, restricted their accessibility. The characteristics of the available prey probably influenced the low success rate of searches conducted in the high pingo zone (Fig. 15).

In contrast, foxes foraging in the meadow zones (especially the short sedge meadow) were most likely to encounter the nests of brant (Mickelson 1975, Eisenhauer and Kirkpatrick 1977) and smaller birds. These birds offered little effective resistence to predation on their eggs by foxes. As a result, search success rate was highest in the short sedge meadow in periods 3 and 4 (Fig. 15).

Significant interactions (Vegetation Zone*Fox, Vegetation Zone*Fox*Success) with implications for fox foraging patterns were indicated by the ANOVA using individual searches as input data. An individual fox whose range was largely comprised of the high and low pingo zones spent more time foraging before terminating an unsuccessful search than did those foxes whose ranges were largely comprised of the meadow zones (Fox 1 vs. Fox 3 and 4; Fig. 10). Fox 1 had the most inland range of all the foxes (Appendix A; Fig. 7). He consistently terminated unsuccessful searches, even outside the pingo zones, after longer periods than other foxes. Fox 4, however, had more familiarity with the meadow zones (Appendix A; Fig. 7). He had the shortest search durations and he demonstrated a similar pattern of unsuccessful search duration whether he was in meadow or pingo microhabitats, despite the longer average search duration overall in the pingo microhabitat (Fig. 11). The experience that a fox had in the habitats with which it was most familiar may have influenced its expectation about overall prey availability ("patch" quality; Krebs et al. 1974, Charnov 1976, see review by Pyke 1984), and it appeared to

retain that expectation while foraging in habitats with which it was less familiar. It should be noted that when search duration values within observation sessions were used in the ANOVA, these interactions were not significant.

Despite the variability in prey availability among vegetation zones, all foxes increased their prey capture rates after birds started nesting in the study area (Fig. 16) and eggs became available. Eggs were apparently taken whenever foxes gained access to a nest, and most were cached singly in "scatter-hoard" fashion (Smith and Reichman 1984) at variable distances from the nest. Only a small proportion of the eggs encountered was eaten immediately. Although our behavioral observations suggested complete specialization on eggs during nesting (Table 8), data from scats (Fig. 20) suggested that the diet of foxes was somewhat more generalized during this time. The scat information should be interpreted with caution because of the difficulty of assigning precise defecation dates and quantifying the number of eggs found in the scats, which restricted the analysis to.the presence or absence of different prey types.

Foxes in the study area probably benefited by switching to egg predation once bird nesting began. They minimized the time and most likely the energy spent conducting searches. They were also able to increase their overall prey capture rate, and were able to store a source of protein and lipids for future use in numerous caches. Seasonally, all foxes within the study area showed the same general foraging pattern; observed differences among individuals were probably related to differences in the specific prey base of the habitats within their ranges.

The Implication of Caching Behavior for Arctic Fox Predation

We observed two types of caching behavior by the foxes in the study area near Kokechik Bay. When a fox captured or located large prey that represented more than one meal (e.g. carrion, adult geese, etc.), the fox ate a portion and buried the remainder in separate caches, a pattern also observed by Macdonald (1976) in experiments with red foxes. The more frequently observed form of caching behavior involved the removal of eggs from nests and their dispersal to other locations in a fox's range. This form of caching represented storage of resources for future consumption (Macdonald 1976, Smith and Reichman 1984).

Not all prey types found in the study area were cached. Foxes always ate microtines when they captured them. Birds usually were eaten when captured and any excess cached, but foxes did not always attempt to capture birds, even when they were within 10 m. This may have been due to the energetic expense of pursuit and handling, the satiation level of the fox (Kruuk 1972), its prey preferences (Macdonald 1976), or a combination of these factors. However, when a fox gained access to a nest, it invariably took the eggs. The number of eggs eaten immediately was low, but the number of eggs cached was apparently limited only by other time constraints of the foxes, such as periodic den visits (in 1985), and maintenance requirements. Because eggs were abundant during the nesting stage and required minimal search and handling time, they were readily cached. The apparently high level of satiation that arctic foxes had for caching eggs, compared to other prey, was similar to that found in red foxes (Sargeant, personal communication) and consistent with Kruuk's (1972) "surplus killing" hypothesis for other carnivores. This hypothesis suggested that satiation will only inhibit hunting behavior, not "catching

and killing" when a carnivore is confronted with prey lacking an "anti-predator" reaction.

Cached eggs in the Kokechik Bay region retained palatability to arctic foxes after storage periods of at least one year. This is comparable to the findings of Sargeant (personal communication) that cached eggs are palatable to red foxes for more than one year. During the pre-nesting stage, foxes retrieved eggs cached in previous summers, a pattern also noted by Braestrup (1941) for arctic foxes in Greenland. The long-term palatability of these caches was probably maintained by burial in cool arctic soils underlain by permafrost (Tieszen 1978, Jackson 1981), which would reduce microbial decomposition (Flanagan and Bunnell 1980).

The ability of arctic foxes to relocate their caches within the study area after varying periods of time was not determined. Macdonald (1976) demonstrated that red foxes retained memory of their own cache locations for at least three days and Burgess (1984) found that arctic foxes in northern Alaska were able to relocate caches (made in June and July) through mid-August. We observed a fox recover two caches in its range during late incubation. However, since the recoveries were made in an area of overlap with neighboring foxes, it was uncertain when the caches were originally made or who made them.

Foxes new to the study area in 1986 were able to locate caches, using olfactory cues, during the pre-nesting stage that had been made by other foxes in previous years. However, Macdonald (1976) found that red foxes had difficulty finding caches made by other foxes, which may explain why arctic foxes in the study area ceased looking for old caches as soon as new eggs became readily available.

The retrieval of caches occurred under two different foraging conditions during the summer. During the pre-nesting stage, when prey capture rates were low, egg caches augmented a fox diet otherwise limited to microtines and carrion.

Late in the nesting stage, foxes started recovering caches at an increasing rate because the number of active nests (and fresh eggs) had declined. in experiments with rodents that cache, Reichman and Fay (1983) found that rodents start feeding on cached food (seeds) when their rate of food harvest drops. Foxes in the Kokechik Bay study area started recovering their caches later in the summer than foxes along the North Slope of Alaska (Burgess 1984) and at a slower rate, suggesting a more abundant prey base in my study area.

Caching has evolved as a means to ensure a stable food supply in a variable environment and the caching period coincides with the availability of excess food (Macdonald 1976, Smith and Reichman 1984). By caching eggs surplus to their immediate needs, arctic foxes in the study area were able to disperse a resource that was clumped both in time and space, in order to use it at a future time, thus stabilizing their long-term food supply. Burgess (1984) suggested that the depletion of caches may influence fox emigration from territories. The abundant egg resource available for caching in the Kokechik Bay study area may result in the less migratory behavior observed on an annual basis in foxes living there (Anthony et al. 1987).

Primary and Alternative Prey

Arctic foxes in the study area near Kokechik Bay engaged in egg predation in both 1985 and 1986, with evidence that the pattern was similar in 1987 (personal observation). Foxes with kits (1985) and those without (1985 and 1986) engaged in similar patterns of egg predation, although parent foxes had greater time limitations affecting their level of egg predation.

The status of the microtine population for the two years of the study differed, however. Microtine population levels were higher during the summer of 1985 (Anthony et al. 1985) than in 1986 (Anthony et al. 1987), although the amount of microtine sign visible after snowmelt in 1986 was greater (Anthony et al. 1987). The amount of sign suggested that microtine population levels were high during the winter of 1985-1986, but our observational data on prey captures and the microtine sign plots sampled in July suggested that microtines had crashed sometime between late May and July, 1986.

High predation rates on eggs, especially those of brant, in both years suggested that eggs were the primary prey during nesting, rather than an alternative to microtines when microtines were scarce. This finding differs from observations made by Summers (1986) and Summers and Underhill (1987) on the winter population status of dark-bellied brant (Branta bernicla bernicla) which nest in the Taimyr Peninsula in the Soviet Union. They suggested that population fluctuations of these brant are correlated with lemming population cycles because of prey switching by generalist predators when lemming populations crash (see also Dhondt 1987, Owen 1987, Greenwood 1987). Other studies supporting the "alternative prey hypothesis" (Angelstam et al. 1984, 1985) suggest that correlations between cycles of microtines and other prey populations are the result of predators exerting more pressure on the alternative prey during microtine population troughs (Hentonnen 1985, Jarvinen 1985, Pehrsson 1986). Fundamental assumptions of this hypothesis are that the predators specialize on microtines when they are available, and the alternative prey types are less numerous or less accessible than microtines (Angelstam et al. 1984). Thus, the alternative prey component of the predators' diet increases only during lows in the microtine population cycle. Despite little available information about microtine population dynamics near Kokechik Bay, the region's

importance as a nesting area (Byrd et al. 1982) ensures that eggs, especially those of brant, are a numerous and highly accessible prey for arctic foxes during the nesting season. Microtines are probably a secondary prey during the nesting stage in all years.

Although foxes do not appear to specialize on microtines during the summer months near Kokechik Bay, microtines may be of primary importance during the winter. Macpherson (1969) suggested that microtine population levels may affect winter survivorship and the subsequent reproductive capability of arctic foxes. Caches may become inaccessible to foxes after the ground freezes, but microtines remain active and available to foxes all winter in the subnivean space (Tast 1966, Mullen and Pitelka 1972). Foxes are able to locate these animals under 75 cm of packed snow (Follmann, personal communication, Mullen and Pitelka 1972). The apparent high population of microtines during the winter of 1985-1986 may have ensured the survivorship of a high number of foxes into the next summer.

Whether the presence of microtines in the study area during the nesting stage acted as buffer on the level of egg predation by arctic foxes cannot be determined from the information collected during the study. Brant had a higher nesting success in 1985 (51%; Stehn et al. 1985) when microtines were present than they did in 1986 (30%; Stehn 1986), when microtine numbers were low. However, interpretation of this finding is complicated by the fact that many foxes in the Kokechik Bay region were raising kits in 1985 (Anthony et al. 1985), but none were in 1986, although a similar number of adult foxes were present (Anthony et al. 1987). Parent foxes in 1985 made periodic visits to their dens. Because whelping dens were located in the pingo zones, travel requirements to and from the meadow zones would have reduced the amount of potential time a parent fox could forage there. Instead, areas near the den may have been used more intensively, as suggested by

Sargeant et al. (1984) for denning red foxes. The distance limitation on possible foraging time in brant nesting habitat may have been reflected in the difference in brant nesting success between the two years. Another complication may have been the different degree of overlap of fox territories between 1985 (little overlap; Anthony et al. 1985) and 1986 (substantial overlap; Anthony et al. 1987). In 1985, prey within the territory of a pair would have been subjected to predation pressure only by that pair. In 1986, however, prey in some areas of the study area would have been subjected to the predation pressure of up to six foxes.

In short, the presence of microtines during incubation in 1985 may have diversified the diet and buffered the impact of foxes on nests, but it did not eliminate egg predation. During both years of the study, eggs, epecially those of brant and other geese, were the primary prey of foxes after nesting was underway (Table 8). Surplus eggs buried in caches augmented the diet of foxes beyond the normal incubation period, and the value of this resource appeared to be independent of the microtine population status.

Arctic Foxes as Predators of Waterfowl

In the study area near Kokechik Bay, arctic foxes had their major impact on waterfowl production by reducing nesting success through egg predation rather than by killing adults or young. During the summer, foxes are active approximately 16 h/d in the Kokechik Bay region (Anthony et al. 1987). The overall median egg capture rate for the nesting stage was 3.5 eggs/h, with 1.0-8.0 eggs/h representing the 25-75% rates. At the median egg capture rate, an individual fox was potentially capable of taking a median of 56 eggs/d (16-128 eggs/d: 25-75% rates), or 2184 (624-4992: 25-75% rates) eggs during the 39 d brant population incubation

period (Sedinger 1986). Of these eggs, at least 80% or 1747 (499-3994: 25-75% rates) eggs would be cached for future use. Although the exact number was unknown, I would estimate that more than half of the eggs that we observed foxes take were those of geese, and mostly those of brant. There were an estimated 2633 brant nests in the study area (assuming an average of 3.5 nests/ha for the short sedge and grass-sedge meadow combined; D. Ward, unpublished data) or approximately 10,795 brant eggs (at 4.1 eggs/nest; Stehn 1986). Assuming that brant eggs represented at least 50% of the eggs taken, foxes 1-4 could account for the loss of at least 4368 brant eggs at the median egg predation rate, or 40% of the total. If the activities of foxes 6 and 7 within the study area are included, the six foxes could account for at least 6552 brant eggs, or 61% of the total.

It is possible that adult birds and chicks were captured at a higher rate in 1985 when their kits were being fed, especially during the brood-rearing period (Appendices B and C), as suggested by Sargeant (1978) for red foxes. Because dens were not visited or observed during the bird nesting stage in 1985, the type of prey arctic foxes took back to the dens during incubation was not known. However, foxes were more likely to immediately consume birds, rather than caching them. Therefore, the number of birds upon which foxes preyed in a given year would remain proportionately small in comparison to their take of eggs.

The impact of arctic foxes upon the nesting success of waterfowl in the Kokechik Bay region is consistent with the observations of researchers studying arctic nesting waterfowl (Barry 1967, Ryder 1969, MacInnes and Misra 1972, Quinlan and Lehnhausen 1982) and geese nesting in the Y-K Delta (Petersen 1984, Sedinger 1984). The results from this study are also consistent with studies on red foxes in waterfowl nesting regions (Sargeant 1972, Sargeant et al. 1984), which showed that predation by foxes had a major impact on the nesting populations of

dabbling ducks. Although the focus of those studies was the impact of red foxes on adult birds, these foxes also take eggs (Sargeant 1972, Sargeant et al. 1984), and red fox kits older than nine weeks were shown experimentally to cache surplus eggs (Sargeant 1978).

As suggested by Sargeant et al. (1984) for red foxes, the arctic foxes near Kokechik Bay benefited by having access to the eggs of birds, such as brant, which were unable to successfully defend them. The probability of egg predation increased during 1986 in range overlap areas, where vulnerable nests were subjected to predation pressures by more than a pair of foxes.

The potential impact of foraging activities by foxes was different with birds capable of defending their nests, such as emperor and white-fronted geese (Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Thompson and Raveling 1987) and supported by studies of snow geese on Wrangel Island (Syroechkovskii 1972). The predation of eggs from the nests of such birds would be largely limited to clutch initiation and during daily recesses from incubation by adult birds (Thompson and Raveling 1987). The lower vulnerability of the nests of emperor and white-fronted geese compared to those of brant to predation by arctic foxes probably contributed to the higher nesting success of the larger geese during both years of the study (Stehn et al. 1985, Stehn 1986).

In general, the foraging behavior, habitat use, and diet of arctic foxes is dependent on the diversity, density and accessibility of prey (Stephenson 1970, Speller 1972, Burgess 1984). Near Kokechik Bay, arctic foxes had access to large numbers of bird eggs during the nesting stage. Many of these eggs, especially those of brant, were vulnerable to predation. The potential impact of arctic foxes on nesting populations of birds was high because of two factors: (1) their tendency to take eggs in excess of their immediate needs, storing the surplus in caches for future use, and

(2) their predation on adult and young birds. Predation by arctic foxes in years when their numbers are high, and especially when they are not raising kits, may exert enough pressure on some species of birds to effectively limit their recovery when their numbers are low.

Implications for Management

Results from this study on the foraging behavior, habitat use, and diet of arctic foxes in the study area near Kokechik Bay indicate that foxes are effective predators of waterfowl. Their tendency to look for and cache eggs surplus to their immediate requirements increases their impact. During bird nesting, non-breeding foxes would have a greater potential for egg predation than would foxes raising kits because non-breeders do not have to return to dens on a periodic basis. Den visits restrict the amount of time available to parent foxes for foraging and potentially restrict the distance travelled by them. However, the food demands of kits after they are weaned would increase the predatory impact of parent foxes on juvenile and molting adult geese. As suggested by Sargeant (1978), birds taken to meet the food requirements of a fox family could represent a substantial proportion of the local population of some species, even if numerically the contribution of a species to fox diets is small. This would likely be the case for species which typically nest at low densities or those whose densities have been reduced by other factors.

Birds that are incapable of defending their eggs from foxes, such as brant, are especially vulnerable to fox predation. Some of the observations from this study suggest that high density nesting aggregations of brant may be less vulnerable to predation, but the relationship between nesting densities and predation needs further study. In areas where vulnerable birds are less numerous, the nests and eggs of the

other geese (cackling Canada, emperor, and white-fronted geese) may be subjected to more fox predation.

Fox numbers fluctuate from year to year. In a low fox year, the impact of foxes may be small. However, in all years, foxes will exert some impact on birds that nest within their range. In years of high fox numbers, especially when there is a large proportion of non-breeders, the large number of ranges and the increased amount of range overlap, will result in a high level of predation pressure, especially on eggs. This predation pressure may be especially severe when prey populations of birds are already at low numbers.

Because the data presented here came from only a small sample of foxes in a restricted study area near Kokechik Bay, the results may only be applicable to a limited geographical area. More work is needed on foxes in other areas of the Y-K Delta, with different habitat components and different prey availabilities, to gain a better understanding of their predation patterns in a broader context. More work on the duration of cache retrieval by foxes through the late summer and fall, and on winter food sources would aid in increasing our understanding of the population dynamics of arctic foxes in the Y-K Delta. Better information on the population dynamics of the local microtines is needed to assess the relationship between microtine population levels, overwintering survival of arctic foxes, fox reproductive capabilities, and the role of alternative prey in buffering fox predation on eggs and young birds.

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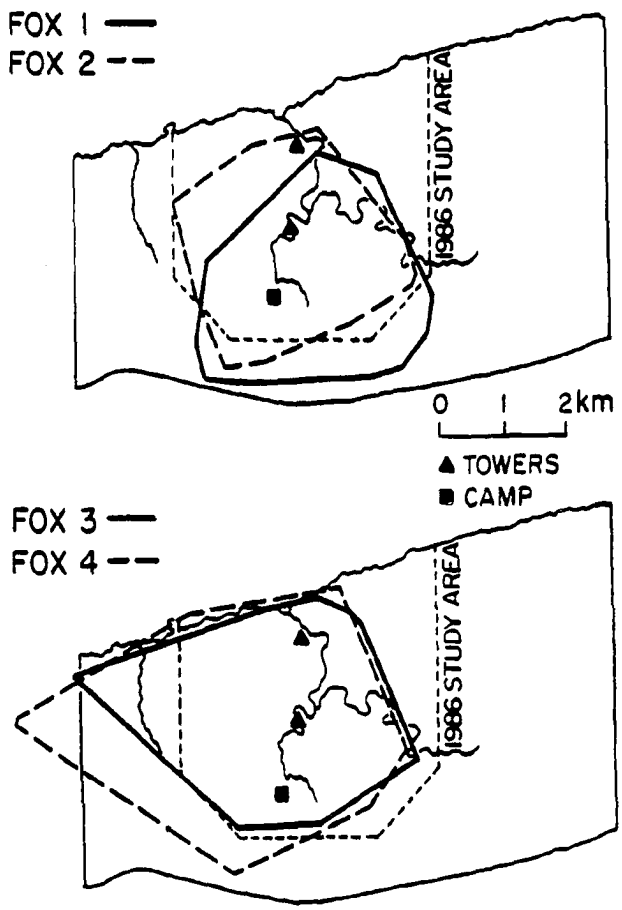
Appendix A. The home ranges of Foxes 1 and 2 (one pair) and Foxes 3 and 4 (another pair) and their location in relation to the 1986 observation area. The collective ranges of each pair constituted a territory. The information presented here was collected by the U.S. Fish and Wildlife Service and is kindly supplied with permission from Mr. Mike Anthony of the Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, Anchorage, Alaska (see also Anthony et al. 1987).



Appendix B. The identification of prey whose remains were collected from the surface of arctic fox dens in 1985 and the date of collection. The listing of prey remains is separated by fox pair groups, identified by their U.S. Fish and Wildlife Service eartag (see Anthony et al. 1985) when possible.

Family Group	Prey Type	Scientific Name	Collection Date
	Brant (juvenile)	Branta bernicla nigricans	12 July 1985
#203	Goose Eggs (2)	Species unknown	12 July 1985
(Female)	Cackling Canada Goose	Branta canadensis minima	22 July 1985
and	Goose Egg	Species unknown	22 July 1985
#226	Cackling Canada Goose	Branta canadensis minima	3 August 1985
(Male)	Brant (juvenile)	Branta bernicla nigricans	3 August 1985
	Birds (2)	Species unknown	3 August 1985
	Green-winged Teal	Anas crecca	26 June 1985
#227	Western Sandpiper	Calidris mauri	15 July 1985
(Female)	Brant (2 juveniles)	Branta bernicla nigricans	5 August 1985
and	Pintail (female)	Anas acuta	5 August 1985
#4 (Male)	Muskrat	Ondatra zibethica	5 August 1985
	Glaucous Gull	Larus hyperboreus	20 July 1985
#223	Emperor Goose	Anser canigicus	22 July 1985
(Female)	Brant (juvenile)	Branta bernicla nigricans	22 July 1985
and	Cackling Canada Goose	Branta canadensis minima	24 July 1985
#2 (Male)	Swan Egg	Cygnus columbianus	3 August 1985
#221			
(Female)	Muskrat	Ondatra zibethica	17 May 1985
and	Tundra Vole	Microtus oeconomus	17 May 1985
#5 (Male)			

Appendix C. The identification of prey brought by parent foxes to the dens during den observations in 1985, and the date of collection. The listing of prey returns is separated by fox pair groups, identified by their U.S. Fish and Wildlife Service eartag (see Anthony et al. 1985) when possible.

Family Group	Prey Type	Scientific Name	Observation Date
	Arctic Tern	Sterna paradisaea	10 July 1985
#203	Gosling	Species unknown	10 July 1985
(Female)	Bird	Species unknown	10 July 1985
and	Gosling	Species unknown	15 July 1985
#226	Gosling	Species unknown	16 July 1985
(Male)	Gosling	Species unknown	18 July 1985
	Goose Egg	Species unknown	18 July 1985
	Bird	Species unknown	11 July 1985
#227	Bird	Species unknown	16 July 1985
(Female)	Gosling	Species unknown	16 July 1985
and	Goose Egg (from cache)	Species unknown	18 July 1985
#4 (Male)	Cackling Canada Goose	Branta canadensis minima	20 July 1985
	Black Turnstone	Arenaria melanocephala	20 July 1985